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VOL. L NOVEMBER–DECEMBER, 1958 No. 6

INTERRELATIONSHIPS AND PHYLOGENY OF THE AQUATIC PHYCOMYCETES [1]

F. K. SPARROW

(WITH 1 FIGURE)

The study of phylogeny always reminds me of the study of the Bible —everyone knows he is an expert and has the final and, of course, only true word. This much can be said however: it rarely fails to provoke heated discussion whether in formal academic confines, or in less formal, smoke-filled surroundings which echo to the clear tinkle of glass and goblet.

Perhaps it is appropriate to ask just what fungi should be considered "aquatic Phycomycetes." It is generally understood that the term "aquatic Phycomycetes" applies to the zoosporic, coenocytic fungi, say, up to and including the Pythiaceae which live in water and soils. This, at least, is my conception of them and they are so regarded here. We cannot, of course, omit mention of the small aberrant genus *Ancylistes*, a group of desmid parasites. These provide us with a beautiful example of adaptive radiation in the fungus kingdom. Here, a few members of a terrestrial group have "gone aquatic," but their reproduction by a conidium popped off above water level betrays their non-aquatic affinities.

No one will question that the Chytridiales, Blastocladiales, Monoblepharidales, Hyphochytriales, Saprolegniales, Leptomitales, Lagenidiales

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and Pythiaceae fall within the aforementioned definition of the group. But what about the Plasmodiophorales? The loose thinking and fruitless argument which have surrounded this group like a miasma are due to a variety of factors, chief of which is the undue weight given to the "plasmodial" nature of the thallus, to protomitotic division figures, and to incomplete and inaccurate observations on critical structures and stages in the life history. Further, the complicated nature of hosts and host tissues in which these fungi have usually been studied does not help matters. Only after Ledingham investigated a member of the order which infected wheat roots, and Couch and his co-workers followed the development of a plasmodiophoraceous fungus parasitic in a simple, coenocytic phycomycete, was it clearly and absolutely established that these organisms bore zoospores in thin-walled sporangia and could most certainly qualify as Phycomycetes. Moreover, these sporangia had no remote resemblance to those of Myxomycetes.

Speculations as to the interrelationships and phylogeny of aquatic Phycomycetes have often been doomed from their inception, by being based upon erroneous observations on structures of significant value, and by giving undue weight to features of dubious importance. Without reviewing the concepts of interrelationships in older and classic works, such as Fischer, Schroeter, C. E. Bessey, deBary, Scherffel, etc., treatises which in themselves were excellent, it seems that the problem of detecting relationships both *within* groups and *between* large groups centers around the selection of the proper and significant morphological units which express these relationships.

For many years I have believed, and still do, that the structure *par excellence* which lies at the very base of any natural system of the lower, aquatic Phycomycetes is the zoospore. Scant attention was given this structure by earlier workers as a criterion of relationship, although it was often accurately protrayed. One cannot but be struck by the fact that when fungus zoospores are compared with motile structures in animals as well as in other plants, they are unique in their type of flagellation. For example, motile structures with only anteriorly directed flagella are the rule in fresh water Algae and in Protozoa. They are rare in fungi.

Investigations in recent years with the aid of modern research tools have greatly added to our knowledge of the precise structure of these swarmers and have served to emphasize with striking clarity the differences between the various types. These have proven of great value in shedding new light on interrelationships. We have:

1. *Posteriorly uniflagellate* type. This type of zoospore is characteristic of the orders Chytridiales, Blastocladiales and Monoblepharidales. Spores of these orders are alike not only in the position of their flagellum, but also in the fact that in a great many their nucleus is shielded, usually anteriorly, by a peculiar structure of unknown function and debatable origin, the "nuclear cap."

Two main variants of the posteriorly uniflagellate zoospore can be recognized, namely:

a) Those bearing for the most part a conspicuous globule in their body; here the swimming movement is frequently of a hopping or gliding type, with occasional recourse to strongly amoeboid creeping; a nuclear cap is usually present and there is monopolar germination. Such zoospores are characteristic of the large group of the Chytridiales.

b) Those zoospores with no conspicuous single globule; swimming evenly, the nuclear cap always present, and often a side body as well; here there is bipolar germination. Such zoospores are characteristic of the Blastocladiales and Monoblepharidales.

Couch (**1941**), using special staining techniques, demonstrated that both of these types of zoospores possessed a flagellum composed of a long thick basal part and a short, thin, whip-lash or tail piece. This so-called "whip-lash" type of flagellum was found characteristic of all representatives of the three orders mentioned.

Manton *et alii* (**1952**) have more recently studied the posteriorly uniflagellate type with the electron microscope and have revealed the finer details of flagellar structure, specifically in *Olpidium brassicae*, a chytrid, and in *Allomyces arbuscula*, of the Blastocladiales.

In both *Olpidium* and *Allomyces* they find that the dismembered flagellum is composed of eleven strands, a central pair and nine peripheral ones.

Koch (**1956**) in dealing with several chytrids belonging to *Chytridium* and *Rhizophydium* has produced even more elegant photographs with the electron microscope of the flagellar apparatus. He finds that the eleven fibrils of the flagellum are themselves composed of parallel subfibrils, the whole being surrounded by a membrane. The whip-lash is simply a prolongation of the central, thinner pair of fibrils, which extends beyond the decreasingly numerous peripheral ones. The flagellar fibrils extend into a blepharoplast, and appear to double back. Koch also gives striking evidence for the presence in the body of the spore of what he interprets as a second, vestigial blepharoplast. If this is the true interpretation of this structure, which was not found in all the

chytrids he investigated, we must take another long look at our ideas of chytrid phylogeny. Koch (**1958**) has also made a careful study of the internal structure of the chytrid zoospore body by means of light microscopy, and has greatly enhanced our knowledge of it. He finds that of the chytrids studied most, but not all, had a nuclear cap. Hence, a nuclear cap is not always present and according to him is not precisely the same structure as in the Blastocladiales and Monoblepharidales.

The Blastocladiales zoospore flagellum, as already indicated, is also of the whip-lash type. Studies of the internal structure of the zoospores of *Blastocladiella* by Stüben, and by Couch and Whiffen (**1942**) reveal the presence of a side body, in addition to a prominent nuclear cap. Such a side body has also been noted by Couch in *Catenaria* and by Richie and Koch in *Allomyces*.

The composition of the nuclear cap has been a matter of considerable discussion. It was first mistaken for the nucleus itself. Mitochondrial origin, and partly nuclear, partly cytoplasmic origin, have been asserted for it. Most recently Turian and Kellenberger (**1956**) in a study of the nuclear cap of the motile gamete of *Allomyces* conclude it to be a transitory accumulation of ribonucleic acid (RNA) associated with sulfhydril proteins. Whatever it is, it is present in nearly all members of the posteriorly uniflagellate series, including the Monoblepharidales, and is to me a strong indication of the interrelationships of the three posteriorly uniflagellate orders.

2. *Anteriorly uniflagellate* type: The second type of uniflagellate zoospore differs radically from the previous one in being *anteriorly* rather than posteriorly uniflagellate. As Couch showed, the flagellum bears along its length, on opposite sides, a series of tinsel-like outgrowths, the whole being referred to as the "tinsel-type" or "Flimmergeisel." The body may or may not bear a fat globule and it may undergo amoeboid changes of shape. What is known of its internal structure indicates that there is no nuclear cap or side body. This peculiar tinsel type of flagellum is typical of the anterior flagellum of all aquatic Phycomycetes, save the Plasmodiophorales.

The anteriorly uniflagellate type of spore is so unlike all the others in structure and motility that the fungi producing it have, with reason, been segregated in an order of their own, which I prefer to call the Hyphochytriales. As indicated by their name, they appear from their body structure, alone, to be true chytrids. Indeed, the instances of parallelisms in body structure between the two groups, Chytridiales and Hyphochytriales, are remarkable.

The zoospores of the remaining Lower Phycomycetes bear two

flagella. There are significant differences, however, between those of the Plasmodiophorales and the remaining biflagellate orders.

The zoospore of the Plasmodiophorales has been demonstrated by a number of competent observers to be unequally biflagellate—i.e., "heterocont." The flagella are apically attached, oppositely directed, and usually very disproportionate in length, so much so that the shorter of the two is often scarcely visible and in some views is completely hidden. In contrast to all other biflagellate fungus spores, these flagella are *both* of the whip-lash type. The longer flagellum is directed towards the rear of the body, the shorter one anteriorly.

The plasmodiophoraceous zoospore, it must be admitted, exhibits features also found in that of true Myxomycetes, such as unequal flagella, both of the whip-lash type. I would not deny that these resemblances are of significance, but I feel they might be explained by an early divergence from a common ancestral type. Furthermore, the inclusion in the "Phycomycetes" of the Plasmodiophorales which, as earlier indicated, bear numerous zoospores in thin-walled sporangia, is as justified as the inclusion in it of the bizarre array of chytrids and their kin.

The last two types of biflagellate swimmers may be formed by one and the same fungus, as in the well-known genus *Saprolegnia*. At this point I wish to interpolate that I have no answer to the riddle posed by diplanetism, or better, dimorphism. Its origin certainly cannot be looked for in monads such as *Leptoderma*, as Scherffel (**1925**) suggests, for, as he admits, this monad is uniflagellate. This is a mysterious sequence, in which a poor swimmer is superseded by a good one.

The first-formed, or "primary," zoospore of the Saprolegniaceae has been variously described, most commonly as "pip-shaped." It has two subapically attached flagella which, when the spore is in motion, are oppositely directed. Couch found these spores to be poor swimmers. The anterior flagellum has been shown by Vlk (**1938**) and Couch (**1941**) by light microscopy and by Manton *et al.* (**1951**) with the electron microscope to be of the tinsel or "flimmer" type, whereas the posteriorly directed one is of the whip-lash type. The cysts formed by these spores after their period of motility have been found by Meier and Webster (**1954**), again using the electron microscope, to have tufts of radiating hairs. The secondary zoospore which emerges from the cyst is again biflagellate. The distinctly shorter flagellum, which is directed anteriorly, is of the tinsel type. This anterior flagellum, like all flagella investigated, has an axis composed of eleven fibrils, two central and nine peripheral ones. The rear flagellum is of the whip-lash type, and has an opaque central axis and massive sheath. The interesting feature

here is that there is considerable reason to believe that in life this flagellum is strongly flattened. If so, the fin-like shape and greater length of the hind flagellum would certainly explain, as has been pointed out, the stronger swimming action of the secondary, as compared with the primary zoospore. Like the anterior one, this flagellum is composed of eleven strands, two central and nine peripheral.

Both Manton *et al.*, and Meier and Webster show that the cysts formed by secondary zoospores after their period of swarming are remarkable for having over their surfaces extraordinary double-headed "boat hooks." Manton and her co-workers found that these hooks have a function in spore dispersal. They noted that such cysts were carried around hooked to motile zoospores, or were joined together into a chain or floating raft.

Meier and Webster (*op. cit.*) further found that in *Saprolegnia parasitica* the secondary cysts bore their hooks at the tips of long tufts of hairs. Extending their study to other genera of the Saprolegniaceae, these same investigators observed in *Isoachlya eccentrica* and *I. unispora* that the cysts were again dimorphic, the primary ones bearing small simple hairs or tufts of hairs, the secondary, short-stemmed hooks. In *Pythiopsis cymosa* and *P. intermedia,* only primary cysts were studied and these were smooth or occasionally had a tuft of hairs. In *Achlya* spp. they were smooth. The secondary cysts of *A. hypogyna* and *A. bisexualis* bore short simple hairs without hooks, whereas in *Protoachlya paradoxa* both types were smooth-walled.

Those genera of the family in which encystment of the primary zoospore occurs within, rather than outside, the sporangia were also studied by Meier and Webster. In species of *Thraustotheca, Calyptralegnia* and *Brevilegnia* their observations were confined to the primary cyst, which they found always to be smooth. In *Dictyuchus sterilis,* where repeated zoospore emergence from secondary cysts was easily induced, they discovered them to be covered with prominent simple spines, the whole resembling in appearance a horse-chestnut fruit.

Differences in cyst ornamentation have suggested to these investigators that this feature may be of value in detecting relationships. Certainly the fact that accompanying dimorphism of the *zoospore* we have dimorphism of *cysts* is a most interesting find. They agree, however, that the evidence from cysts is still too fragmentary to lead to any sweeping conclusions with respect to interrelationships.

We come now to a consideration of interrelationships within the large groups, usually taxa of ordinal rank.

In characteristic human fashion I will take up the easiest ones first.

Speaking broadly, the Saprolegniacean-Lagenidiacean-Peronosporacean series of orders—i.e., biflagellate zoosporic forms with nearly equal, oppositely-directed flagella—seem to be composed of related fungi, related by zoospore structure, formation in succession of two types of swarmers or vestiges of this, zoospore behavior, wall composition, and usually well-marked oogamous sexual reproduction.

Within this series there are three families whose members have probably been reduced to a chytrid-like body structure; namely, the Ectrogellaceae, Olpidiopsidaceae and Thraustochytriaceae. Indeed, species of the first two families long enjoyed full status as *bone fide* chytrids. I cannot, therefore, follow Scherffel (**1925**) here in believing the Ectrogellaceae "primitive." In the Thraustochytriaceae we have an unusually striking instance of the assumption, by reduction, of the chytrid habit. Now that another genus and species of the family have been discovered by Kobyashi and Ookubu (**1953**) and with Johnson's (**1957b**) new observations on *T. proliferum*, there is no question from their findings but that the interpretation of these forms as reduced saprolegniaceous fungi is correct.

These biflagellate fungi—i.e., of the Saprolegniacean-Lagenidiacean-Peronosporacean series—present relatively little trouble when visualized as a group which has arisen from a single ancestral stock. Whether this was from siphonaceous algal stock, strongly oogamous, and perhaps *Vaucheria*-like in nature, as has long ago been suggested, or was directly from monad ancestry, from types suggested by Scherffel (**1925**)—for example, *Pseudospora, Amylophagus,* etc., with two flagella, central vacuole in the developing sporangium, and simultaneous cleavage of peripheral cytoplasm to form zoospores—poses an interesting question. Which of these origins is correct, if indeed, either is, I would not attempt to say. I have never been an adherent of the idea that Phycomycetes, as a whole, have been derived from algae by loss of chlorophyll. On the other hand I have never closed my mind to the possibility that within this complex called "Phycomycetes" there may, indeed, be groups of algal origin. It seems possible, considering the resemblance of *Vaucheria* in vegetative structure and sexual reproduction to saprolegnians, that it and the entire Saprolegniacean-Lagenidiacean-Peronosporacean series may, indeed, be related, as supposed by many early mycologists. Investigations, again by Koch (**1951**), on the flagellation of the only simple, uninucleate swarmer produced by *Vaucheria,* the sperm, show that it bears a striking resemblance to a saprolegniaceous zoospore, even to the point of being colorless. There are two oppositely-directed, subapically attached flagella, the anterior, slightly shorter one,

being of the tinsel type, and the posterior longer one of the familiar whip-lash type.

We come now to face the most difficult task of all, namely, the interrelationships and phylogeny of the posteriorly uniflagellate series—i.e., Chytridiales, Blastocladiales, and Monoblepharidales. These, you will recall, while being alike in having a posterior flagellum, etc., are exceedingly diverse in body plan, method of development, zoospore discharge, internal structure, sexuality and life history. In these features they are also in my opinion so strikingly different from other "Phycomycetes" as to warrant their exclusion, along with the Plasmodiophorales and Hyphochytriales, from this class of fungi.

The first order, and certainly the most complex, complex because it probably embraces within itself diverse groups, is the Chytridiales. I need not repeat the harsh words uttered in the past about these dazzling and elusive creatures. These epithets have been multitudinous, vigorously expressed, and usually justified. Chytrids are minute, here today and gone tomorrow, recalcitrant wherever and whenever the opportunity offers, and all in all, thoroughly uncooperative. They have left generations of skilled mycologists wondering in their final hours if they really *had* seen such and such a chytrid forty years ago, for it had never afterwards been seen! One need only cite the cases of the orange-red *Zygochytrium* and the blue *Tetrachytrium*, described 84 years ago by Sorokin from Russia, and not seen since. Although commonly ascribed by less imaginative mycologists to one of Pierre Smirnoff's early successes in the distillation of potato mash, most chytridiologists have faith that these fungi will be found again. Indeed these men are ready, and more than well-equipped, as, perhaps in like manner, was Sorokin, to resume the hunt.

We have once more to ask ourselves here, just what characters are pertinent in detecting interrelationships among the chytrids? Are there underlying developmental or morphological features, vegetative, reproductive, or both, upon which we can place reliance?

First of all, holocarpy and eucarpy. The families Olpidiaceae, Achlyogetonaceae and Synchytriaceae are all endobiotic and holocarpic —i.e., they are within the host cell and lack any specialized structures for nutrient-gathering. In these families the entire thallus functions for reproduction. Such holocarpy is encountered elsewhere in the lower Phycomycetes, notably in the Plasmodiophorales, Ectrogellaceae of the Saprolegniales, Olpidiopsidaceae, Sirolpidiaceae and Lagenidiaceae. Holocarpy, therefore, appears at various levels of Phycomycete evolution, not just in the Chytridiales. Although holocarpy may appear occa-

sionally, atypically, in certain eucarpic chytrid genera with elaborate vegetative development (*Physoderma*, for example), it seems a good character for use in determining relationships within the chytrids, and the grouping together of holocarpic forms seems justified.

The remaining families of the Chytridiales are all "eucarpic"—i.e., in addition to one or more reproductive rudiments there is some sort of specialized, strictly vegetative system, which does not participate in reproduction. In chytrids this is nearly always a branched complex of strongly tapering rhizoids. Whether the holocarpic forms have been derived from these eucarpic types by reduction, or whether the simpler forms are, indeed, direct derivatives from monad ancestral stock, as their primitive type of sexuality would suggest, and have in turn, given rise to eucarpic forms, is at present a moot but intriguing question. Eucarpy most certainly seems a distinct evolutionary advance over anything found in the supposed monad ancestral stock and the grouping together of eucarpic chytrids seems eminently suitable.

The nearly fifty genera and hundreds of bizarre and diverse species of *eucarpic* chytrids make it difficult indeed, to trace their interrelationships. The following features seem, however, of value here: first, type of thallus, whether monocentric (i.e., with one reproductive rudiment) or polycentric (i.e., with several reproductive rudiments); second, sequence of thallus development; third, type of sexual reproduction; fourth, type of zoospore discharge—i.e., whether inoperculate or operculate.

(1) *The type of thallus produced.* Although this would seem a most obvious character in which to detect relationships, it is not, to my mind, of the same worth here as was the zoospore at the class level. This may be seen by comparing the thalli found in the Blastocladiales and Chytridiales. In the former, the vegetative plant may be plasmodial, as in the Coelomomycetaceae, chytrid-like, as in *Catenomyces, Catenaria,* and especially certain forms of *Blastocladiella;* or definitely mycelial, as in *Allomyces.* In the chytrids, it may, again, be plasmodial as in *Rozella,* walled and rhizoidal as in most chytrids, with a basal cell, rhizoids and reproductive rudiment, as in *Macrochytrium* and *Cylindrochytridium,* or mycelial, as in *Megachytrium, Coenomyces* and *Aphanistis.* In other words, the same thallus types are repeated in the several taxa.

A great number of eucarpic chytrids develop only one center of reproductive activity. Variations have been noted occasionally, but usually this feature, where studied, is a constant one for a particular fungus. Such "monocentric" chytrids seem to form a well-defined unit of relatively simple-appearing fungi. No doubt in the future some will

be shown to be merely reduced types. A lesser number develop more than one reproductive rudiment on a thallus and certainly appear to be of a higher level of organization than monocentric ones. These "polycentric" types are rightly segregated from their simpler allies at the family level, as for example, the Cladochytriaceae and Megachytriaceae.

(2) *Sequence of thallus development.* Like sexuality, which I will discuss in a moment, this gave hopes of being a feature of sufficient constancy to be of value in detecting interrelationships within the chytrids. Intensive work during the past 15 years, however, has not borne out the occurrence of any such constancy. Thus, in the case of a particular morphologically well-defined chytrid (*Diplophlyctis intestina,* for example), two eminent investigators may differ markedly on its pattern of development, and will sometimes, unknowingly, even later disagree with their own earlier observations. Probably, they were correct in all instances; it was the chytrid which was uncooperative!

(3) *Sexual reproduction.* One would have expected the type of sexual reproduction to be of value in detecting relationships, but this does not seem to be true. Type of sexual reproduction has, in fact, proved somewhat confusing as a criterion of relationship, at least in eucarpic chytrids. From what is known of holocarpic chytrids they all possess a type of sexual reproduction involving fusion of motile gametes. This was the type of sexuality which might be expected to prove typical for eucarpic chytrids as well, but such has not been the case. We find authenticated instances of sexual reproduction in eucarpic chytrids usually to be by some sort of conjugation process in which one or, more often, both gametes have come to rest and become immature gametangial thalli. When they are joined by the other gamete, the latter does not seem to lose its identity as a gametangial plant and indeed, may form rhizoids. Other types of conjugation are known, such as those in *Siphonaria, Diplophlyctis,* etc., where anastomosis of rhizoids occurs; *Polyphagus, Zygorhizidium,* etc., where conjugation tubes are produced; or *Endocoenobium,* where direct adnation of thalli produces a bud which enlarges as it receives the contents of the conjugants. In all cases the receptive structure becomes a resting spore.

In *Physoderma,* a chytrid genus of obligate parasites of vascular plants, which by its elaborate, dimorphic thallus structure (if we take this as a criterion) has affinities with the polycentric Cladochytriaceae as well as monocentric Phlyctidiaceae, there is now ample evidence to indicate that we are dealing with a group of eucarpic chytrids with isogamous motile gametes, and alternation of heteromorphic generations. That is, we have an epibiotic monocentric gametangial stage and an endo-

biotic, probably diploid, polycentric resting spore stage. Here, extreme elaboration of the eucarpic body is combined with a primitive type of sexuality by means of fusion of isogamous planogametes such as is found in simple, holocarpic chytrids.[2]

(4) We come now to *type of zoospore discharge* as a criterion of relationships. In a few quarters the raising of this feature to a place of high order in detecting interrelationships has been questioned. I must confess that just as the type of zoospore and its associated features have impressed me for many years as being of significance in detecting relationships, so also, at least in eucarpic chytrids, has the method of sporangial discharge. The recognition of this feature as a criterion of relationship, within both monocentric and polycentric eucarpic chytrids has, I believe, proven eminently justified and useful. The deliquescence at zoospore liberation of a plug of modified wall material—i.e., inoperculate discharge—is a distinctly different process from the circumscissile dehiscence of an operculum derived from wall material, which, in the case of epibiotic chytrids, is in fact a portion of the original zoospore cyst. No single chytrid has ever been found which has both methods of discharge. Here is a character which is absolute in its constancy.

In recent years the term "endooperculum" has been applied by some to a structure of different origin from the aforementioned operculum. In certain chytrids, often those with a prominent gelatinous "plug" in the discharge tube, a membrane may form over the face of the protoplasm which after deliquescence of plug is exposed at the base of the tube within the sporangium proper. This membrane may become, often with time in quiescent cultures, rigid, and even umbonate. Such a structure has been found in both inoperculate and operculate types of chytrids and even in the Blastocladiales (*Catenomyces*). Haskins (**1948**), who made an extensive study of endoopercula in the ubiquitous *Rhizophlyctis rosea*, where they were said to be uniformly produced, found that zoospore discharge often took place before there was any evidence of them. Furthermore, in discussing zoospore discharge in *Diplophlyctis sexualis*, he states (**1950**): "Our species in rapidly growing cultures dehisces in a normal inoperculate manner and occasionally after extrusion of a gelatinous plug, but in older, stagnating cultures, after the deliquescence of the gelatinous tip of the exit-tube has occurred, the membrane between the protoplasmic content of the sporangium and the external medium thickens. This membrane may thicken so as to form an endo-operculum-like structure, which at subsequent dehiscence of the sporangium may

[2] Such gametes have been shown to be present in *Physoderma lycopi* by Sparrow, and in *P. pulposa* by Y. Lingappa.

merely rupture or may be forced out as a cap. . . ." From these observations and our own on certain species of polycentric chytrids we concur with Hanson (**1945**) who, in discussing the relationships of *Catenomyces* (which we prefer to put in the Blastocladiales rather than the Chytridiales), states that the endooperculum is a "generically invalid" character. It can probably be found in many chytrids under certain environmental conditions. The term "operculum" should be reserved for a definite and discrete structure which is an actual part of the sporangium wall.

I feel that operculate and inoperculate eucarpic chytrids represent two distinct lines of chytridiaceous fungi which have undergone parallel evolutionary development. Whether operculate forms have been derived from inoperculate types, or whether they have arisen directly from some as yet unknown operculate, monad group and undergone parallel development with inoperculate forms, we cannot be sure. The absence of any holocarpic operculate types can be explained by either of these postulates.

Turning to the remaining orders of posteriorly uniflagellate zoosporic groups we have a somewhat easier task. In the Blastocladiales we have an order of fungi united as indicated earlier by several very clear-cut characteristics, namely, zoospores with a massive nuclear cap, often with a side body as well, bipolar mode of germination and resting spores with thick punctate walls.

These criteria of relationships of blastocladiaceous fungi are, indeed, fundamental ones, and have enabled us to recognize, for example, that certain supposed chytridiaceous fungi actually belong to the Blastocladiales. Such instances have been due primarily to the astute observations of Couch. An outstanding example is that of the Coelomomycetaceae, a group of obligate parasites of insect larvae. Here, by a study of the resting-spore structure, its mode of germination and structure of the zoospore, Couch (**1945**) showed that these fungi, which have an unwalled, plasmodial type of vegetative thallus, were not chytrids as supposed, but members of the Blastocladiales.

The Blastocladiales, considered by Scherffel as possibly a branch of the line culminating in the Monoblepharidales and arising from unknown monad ancestry, is, to my mind, closely allied to the Chytridiales. Not only do chytrid zoospores show a strikingly similar internal organization to that of the Blastocladiales, a whip-lash flagellum, etc., but chytrid rhizoids and those formed by such genera as *Allomyces* and *Blastocladiella* show remarkable structural similarities. Indeed, those who have observed a species of *Blastocladiella* grown under poor nutrient conditions are struck by its strong resemblance to a monocentric, rhizi-

diaceous chytrid. Other features, as well, such as lack of completely cellulose walls, method of formation of resting spore, etc., seem to unite them. The presence of alternation of generations in certain of the Blastocladiales is not a barrier in deriving one order from the other. For one thing, I am convinced that there exist among the chytrids numerous instances of such alternation which are as yet undetected. For example, referring again to *Physoderma*, alternation of generations has been morphologically proven to occur in this chytrid genus.

The final order of the posteriorly uniflagellate line, the Monoblepharidales, is characterized by several striking features which it shares with its relatives in the Blastocladiales, namely, protoplasmic structure, swarmers with a strongly developed nuclear cap, and bipolar zoospore germination. Like most of its chytridiaceous ancestors, however, the only diploid plant is represented by the mature, encysted, one-celled zygote, which presumably undergoes meiosis before germination. Here, then, the body is haploid and no alternation of haploid and diploid vegetative plants occurs.

Within this small but fascinating order are three genera, *Gonapodya*, *Monoblepharella* and *Monoblepharis*. By not recognizing the fundamental significance of zoospore structure, *Gonapodya*, because of its thallus, was long placed in the Saprolegniales, and later in the Leptomitales along with other segmented, hyphal forms. By others it was put in the Blastocladiales. Its alveolate, or foamy, disposition of the protoplasm, and the internal structure of the zoospore, seemed, however, more nearly to ally it with *Monoblepharis*. Until its sexual reproduction was found, however, a strong element of doubt prevailed. Johns's and R. K. Benjamin's (**1954**) discovery that both species of *Gonapodya* had a type of sexuality essentially like that of *Monoblepharella* was a rare example of the use of similarity of sexual reproduction to detect relationships.

Clearly, we see in the Monoblepharidales the assumption of quasi-oogamy and true oogamy of a type quite different in origin from that evolved by the Saprolegniacean-Lagenidiacean-Peronosporacean line. There are other, more elusive, bonds between the Monoblepharidales and the Blastocladiales, and these will, I feel certain, be clarified in the future by discoveries of other types of sexuality.

The Monoblepharidales did not, however, in my opinion, give rise to any higher groups of fungi, and to my mind stand as a terminal group of what may be called the "Chytridiomycetes," which possibly has evolved from monad ancestral types, such as *Aphelidium*, as indicated by Scherffel (**1925**).

I wish to re-emphasize that the Hyphochytriales, with zoospores bearing a single anterior flagellum of the tinsel type, stands alone, and has arisen from wholly different ancestral stock from other Phycomycetes. There are many protozoan types from which it could have evolved.

Similarly, in the Plasmodiophorales, whose swarmers bear two unequal flagella of the whip-lash type, we have an isolated group, probably of protozoan origin, and Karling's (**1944**) suggestion that some monad similar to the marine *Phagomyxa* might be the ancestral type has much merit.

Summarizing, if we define broadly the aquatic Phycomycetes as "coenocytic aquatic, semi-aquatic or terricolous fungi with zoospores formed in thin-walled sporangia," we may include even the Plasmodiophorales. Perhaps to add that they are aquatic or semi-aquatic is implied in their formation of zoospores, clearly structures adapted for travelling through liquids. Indeed, even most lower Phycomycetes which are obligate parasites of vascular land plants need free water to infect their hosts, thus betraying their purely aquatic ancestry. On the other hand, we might better recognize that the "Phycomycetes" are not a homogeneous monophyletic group but rather an artificial category of coenocytic, zoosporic fungi (FIG. 1). Within them we can clearly delineate, primarily by means of the zoospore structure, and other asso-

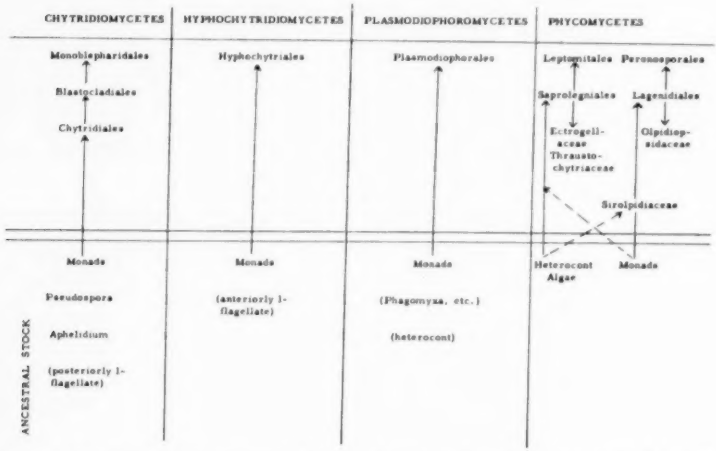

FIG. 1. Chart indicating suggested lines of descent of the fungi now comprising the "Aquatic Phycomycetes" (exclusive of the Ancylistaceae, Entomophthorales).

ciated features as well, four streams, or better, galaxies, of organisms which to my mind have come from radically different progenitors, possibly single-celled, free-swimming forms even now extant: (1) *Chytridiomycetes*, with posteriorly whip-lash uniflagellate zoospores and associated characters already mentioned, with a diversity of types of thalli and sexual reproduction, culminating in the oogamous *Monoblepharis* which apes to a degree the oogamy of the Saprolegniacean-Lagenidiacean-Peronosporacean line; (2) *Hyphochytridiomycetes*, with a single anterior tinsel flagellum, with body types paralleling those of Chytridiomycetes and in the only well authenticated case of sexuality known (Johnson, **1957a**) resting-spore formation after conjugation of like thalli; (3) *Plasmodiophoromycetes*, with plasmodial thallus, protozoan-like (not Myxomycete-like) nuclear-division figures, and biflagellate, heterocont zoospores, with both flagella of the whip-lash type; derived perhaps, as has been suggested from organisms similar to plasmodial, marine, *Phagomyxa*-like forms with heterocont zoospores; (4) *Phycomycetes*, the Saprolegniacean-Lagenidiacean-Peronosporacean galaxy, with strong, true mycelial development, with diplanetic, biflagellate zoospores with oppositely directed nearly equal flagella, the forward of the tinsel type, the posterior of the whip-lash type, and with well defined oogamous sexual reproduction, but never with motile flagellated sperm nor motile egg or zygote.

The aquatic Phycomycetes, in this restricted sense, may, as earlier suggested, have all come from heterocont algal stock. Another possibility is that the Saprolegniaceans only are from algal stock and that the Lagenidiacean-Peronosporacean series had their origin either directly from biflagellate monads, or by way of such generalized marine forms as *Sirolpidium* or *Pontisma*. Both of the last-named genera show rudimentary mycelial formation, yet can appear like an *Olpidiopsis*. However, lack of knowledge of their sexual stage hinders further development of this line of reasoning.

It would be nice to feel that the basic zoosporic groups could be as logically arrived at as Ernst Bessey suggested in his presidential address to our Society in 1942; namely, by starting with a heterocont unicellular alga, and after loss of chlorophyll and the anterior flagellum obtaining a chytrid; or by losing the posterior one, producing a hyphochytrid; or by retaining both, deriving the Saprolegniales-Peronosporales line. I feel, however, that the facts point to a more complex answer than this. Just what the answer is must await the future. As illustrative of new, experimental approaches to this problem I call your attention not only to the use of the electron microscope by Manton, Koch and others, and

the histo-chemical approach by Turian and Kellenberger, but also to E. C. Cantino's (**1950, 1955**) two excellent starts at the construction of a physiological phylogenetic tree. A forthcoming publication by G. S. Kilsheimer and B. Axelrod presents another challenging approach to the study of phylogeny. Their preliminary work, using crude extracts, indicates that the action of acid phosphatases of undoubted plant origin (ginkgo seed, cabbage) is not inhibited by (+)-tartaric acid, whereas that of acid phosphatases of animal origin is. Among the organisms investigated were several Phycomycetes and it is of interest to us here that forms such as *Rhizopus* and *Mucor* were definitely plant-like in their response to the inhibitor, whereas species of *Blastocladiella, Pythium* and *Phytophthora* reacted in animal-like fashion.

Not only are these vigorous new attacks on the central problem, but they show mycologists that there are among us those who can crawl above the biochemical and physical quagmire and breath the stimulating and rarified ozone of phylogenetic speculation, hitherto thought to be the exclusive preserve of the morphologists.

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SOME LEAFSPOT FUNGI ON WESTERN GRAMINEAE—XII [1]

RODERICK SPRAGUE [2]

(WITH 2 FIGURES)

This paper is based largely on a study of grass disease specimens obtained in the Far West. A few noteworthy collections were made in June and July, 1957 in the Priest River and Priest Lake areas in Idaho and in adjacent Pend Oreille Co., Washington. Some specimens were gathered in the mountains of north central Washington in August of 1957. Many packets were obtained in late August and early September in company with G. W. Fischer in the mountains of Oregon, California, Nevada, Arizona, Utah and Idaho. Owing to opportune rains in northern Arizona, the collecting in the vicinity of Flagstaff was especially rewarding. Only part of the late summer material will be discussed here; the remainder awaits later study. Unless otherwise mentioned, all material gathered in August and September, 1957, was collected by Fischer and the writer and filed with a WSP number in the Plant Pathology Herbarium, Washington State College, Pullman, C. G. Shaw, Curator.

Mycosphaerella cinnafolia sp. nov.

Maculis luteis, emarginatis, peritheciis seriatim dispositis, numerosis, globosis, erumpentibus, brunneis, 60–100 μ diam., ostiolatis; ascis clavatis, 20–30 × 9–11 μ; ascosporulis 8, hyalinis, subfusiformibus, 1-septatis, 11.3–14 × 2.5–3.4 μ.

Spots buff, covering most of infected leaves; perithecia very abundant, in lines, globose, brown, with well defined ostioles, strongly erumpent, 60–100 μ diam.; asci short, club-shaped, 20–30 × 9–11 μ; ascospores 8, hyaline to faintly yellow-tinted, somewhat pointed at both ends, 1-septate, 11.3–14 × 2.5–3.4 μ.

Hab. on living to necrotic leaves of *Cinna latifolia*, near Battle Mountain State Park, Blue Mts., Oregon, in brush along a small creek, leg. *R. Sprague and G. W. Fischer*, Aug. 21, 1957 (WSP 42871), TYPE.

[1] Scientific Paper No. 1701, Washington Agricultural Experiment Stations, Pullman. Project No. 449.

[2] Pathologist, Washington State College Tree Fruit Experiment Station, Wenatchee.

This fungus resembles *M. deschampsiae* Sprague (**20**) but differs in having somewhat pointed spores. The specimen, however, is somewhat plasmolyzed and spore structure is not clearly defined in much of the material. The perithecia on the leaves are many; one leaf showed over 6,000 perithecia.

Except for the possible relationship to *M. deschampsiae,* this fungus is distinct from any known. Mature material of *Mycosphaerella* spp. on living, current-season grass leaves is not common and on *Cinna* is unknown to the writer. The only comparable material on *Cinna* is an undetermined collection from Tlingit Point, Alaska, of an immature (cf. WSP 33752; 37091) "perithecial" fungus (**21**).

The type locality is a small marshy area along a wooded rill just below Battle Mountain State Park on U. S. Highway 395 in Umatilla Co., Oregon.

Leptosphaeria georgius-fischeri sp. nov.

Maculis diffusis, evanescentibus, foliis aureis; peritheciis dispersis, brunneis, globosis, ostiolatis, 57–120 μ diam.; ascis clavatis, 38–45 × 12–15 μ; ascosporulis 8, fusiformibus, triseptatis, chlorinis, 17–25 × 5.5–6.8 μ.

Spots diffuse, soon fading, originally narrowly elliptical but most of the perithecia occurring on yellowed leaves on living plants; perithecia scattered, dark brown, globose, ostiolate, 57–120 μ diam.; asci clavate, short, 38–45 × 12–15 μ; ascospores fusiform, constricted somewhat at the three septa, yellow to chlorine, scarcely brown, 17–22 × 5.5–6.8 μ.

Hab. in living leaves of *Muhlenbergia filiformis,* near Vidae Cliffs, Crater National Park, Oregon, Aug. 23, 1957, leg. *Sprague and Fischer* (WSP 42933), TYPE.

This fungus is named for George W. Fischer, who has been my colleague on a number of extensive collecting trips in the Western States and through whose official capacity most of these trips have been made possible.

This material was found in a slight depression in a tiny opening near the edge of a conifer forest in Crater National Park. The partial shading apparently aided the weakly parasitic fungus. Nearly all the lesions had lost their original outline, fading into the general yellow of the dead leaf parts. A few discolored spots were still observable as narrowly elliptical streaks on the filiform leaves of the host.

This material proved difficult to determine. In some ways it is close to my *Leptosphaeria muirensis* (**21**), but the symptoms are distinct and all components, except the spores, are smaller. The spores of *L. muirensis* tend to be flattened on one side, those of *L. georgius-fischeri*

scarcely so. While one might consider the Crater Lake material as a variety or form of *L. muirensis,* it seems to me simpler to recognize it as distinct for the reasons cited above plus the additional great differences in both geographical and host range.

L. georgius-fischeri was compared critically with *Metasphaeria culmifida* (Karst.) Sacc. (**18**; **15**, v. 2, p. 174) which has yellow spores 21–25 × 6–8 μ. However, this species has large perithecia, 180–240 μ diam. and asci 75–95 × 14–15 μ. This fungus, according to Lind (**8**; **9**; **10**), is the perithecial stage of *Septoria culmifida* Lind on *Phleum pratense* L. Grove placed *S. culmifida* under *S. oxyspora* (**4**) and we placed this under *Selenophoma donacis* var. *stomaticola* (Baüml.) Sprague and A. G. Johnson (**26**).

In addition to comparing *L. georgius-fischeri* with the *Metasphaeria* above mentioned, I also considered *L. muhlenbergiae* Rehm (**14**; **15**, v. 24, pt. 2), which was originally found on *Muhlenbergia racemosa* in North Dakota. It has spores 30–35 × 6–7 μ and asci 140 × 215 μ, and thus is greatly different from our fungus. Another *Leptosphaeria* on *Muhlenbergia, L. associata* Rehm, occurs with *Epichloe* and has asci 75–90 μ (**13**; **15**, v. 24, pt. 2). I also considered the common and well-known fungus *L. microscopica* Karst. (**7**; **15**, v. 2, pp. 59–60). It also has larger asci, 80 × 16 μ, and fusoid oblong spores. We encountered, incidentally, another species of *Leptosphaeria* in the type material of *L. georgius-fischeri.* The unknown had brown cylindrical spores 25 × 9 μ, on older leaves. If encountered in future studies care should be taken to segregate it from *L. georgius-fischeri.* A slide mount of the brown-spored *Leptosphaeria* is included in WSP 42933 and is labelled "*L.* sp., not *L. georgius-fischeri.*"

In one mount of *L. georgius-fischeri,* I encountered tiny arcuate microspores 4–7 × 0.8 μ. Further examination showed that they were derived from ill-formed acervuli widely scattered over the yellowed leaves and associated with developing perithecia. These microspores may be part of the life cycle of *L. georgius-fischeri.* Classification of this fungus was also difficult and uncertain. The spores resemble *Libertella* Desm. but that genus is usually pseudolocellate. In Clements and Shear the fungus keys to *Glocosporium* (**2**) .In the Von Arx revision (**1**) it comes closest to *Colletotrichum,* except for spore size. The conservative, if not entirely satisfactory, disposal is to assign the fungus to *Colletotrichum,* especially because it is likely a phase of the *Leptosphaeria.*

Colletotrichum georgius-fischeri sp. nov.

Acervulis subhyalinis, 50–100 μ diam.; conidiophoris hyalinis, brevifiliformibus, 10–14 × 1.0–1.5 μ diam.; sporulis arcuatis, hyalinis, aseptatis, 4–7 × 0.8 μ.

Acervuli obscure, sub-hyaline, 50–100 μ diam.; conidiophores hyaline, relatively short rod-shaped, 10–14 × 1.0–1.5 μ; spores arcuate, hyaline, aseptate, 4–7 × 0.8 μ.

Hab. in living leaves of *Muhlenbergia filiformis* with the type of *Leptosphaeria georgius-fischeri*. A labelled glass slide numbered WSP 42933 is the HOLOTYPE of *Colletotrichum georgius-fischeri*.

Colletotrichum sierraensis sp. nov.

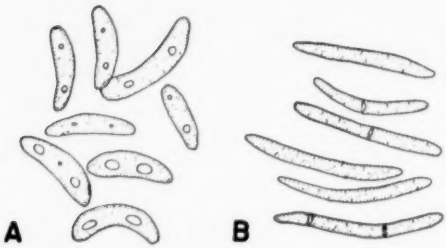
Macuis foliicolis, stramineis v. avenaceis, emarginatis; acervulis hyalinis, subsuperficialibus, amphigenis, 250–500 × 80–120 μ; conidiophoris hyalinis, 5–7 × 1.2 μ diam.; conidiis hyalinis, curvulis, allantoideis, phaseoliformibus v. subphaseoliformibus, variabilibus, numerosis, vacuolatis, 10–17 × 2.8–4.2 μ.

Spots on leaves straw colored, indefinite, without margin, rarely elliptical; acervuli hyaline, arranged in lines, somewhat superficial; when mature definitely emerging from the leaf tissue, mostly filling the epidermal cells of the underside of the leaf but mycelium penetrating through the leaf and forming acervuli at times on the upper epidermal cells, 250–500 × 80–120 μ; conidiophores abundant, linear, 5–7 × 1.2 μ; spores hyaline, white in masses on acervuli, giving the latter their white appearance, spores curved to nearly straight, rounded on each end, sausage-shaped, bean-shaped or irregularly bean-shaped with aberrant forms present, vacuolate (pseudo-septate, in part) 10–17 × 2.8–4.2 μ.

Hab. on basal leaves of the annual *Poa bolanderi*, Big Meadows, Calif., Aug. 29, 1957 (WSP 42900), TYPE.

This material is not very striking in appearance; in fact I almost discarded it before locating the fungus. The lesions are obscure and the fungus tissue is hyaline. The acervuli are characteristically arranged in vein-delimited rows like very fine machine stitching done with white thread on lightly tinted cloth. The fungus is very different from any known on Gramineae. I have followed Von Arx in assigning this to *Colletotrichum* (**1**). Von Arx has rejected *Glocosporium*, assigning fungi so named to a number of genera in Melanconiales, Moniliales and even Sphaeropsidales. Because he apparently does not believe that setae are mandatory for assignment to *Colletotrichum*, our fungi are assignable to that genus, sensu Von Arx.

C. sierraensis has spores (FIG. 1, A) similar to *Glocosporium meinersii* Sprague (**18**, fig. 1, F). However, Von Arx places this latter fungus in a new genus *Rhynchosporina* V. Arx which he created for this species. *R. meinersii* produces its stromatic tissue internally, penetrating by means of narrowed conidiophores through the cuticle of the leaf. Von Arx based his study on the type on *Phleum alpinum* L. The variety on *Poa alpina* L., which he does not discuss, should be known as *Rhyncho-*



All drawings in FIG. 1 are × 1000, done with the aid of the camera lucida. FIG. 1, A. Conidia of *Colletotrichum sierraensis*, TYPE. FIG. 1, B. Atypical pycnidiospores of *Septoria infuscans* on *Elymus canadensis*, Pump House Wash in Oak Creek Canyon, Ariz., Sept. 1, 1957.

sporina meinersii (Sprague) Von Arx var. **alpina** (Sprague) comb. nov. (*G. meinersii* var. *alpina* Sprague, Mycologia **41**: 494. 1949.)

An illustration of the acervulus development in *C. sierraensis* is shown in FIG. 2. In this case the acervuli have formed on opposite sides of the leaf, the mycelium penetrating through the leaf between the veins.

BALANSIA STRANGULANS (Mont.) Diehl was found on *Phleum pratense* L. near Lapine, Oregon, on Aug. 22, 1957 (WSP 42872). The striking black collar of imbedded perithecia occurred at the base of one fruiting grass head and on an adjacent leaf (FIG. 2, E). Detailed search in the meadow failed to locate any other material except one partially aborted additional head. The fungus was also found on timothy a few days later in California near Lake Mono (WSP 42873). The host is unreported for this fungus. The fungus, according to Diehl's careful study, has not been found nearer than Nebraska and Kansas (**3**).

ERYSIPHE GRAMINIS DC. ex Merát is common locally on *Agrostis variabilis* (Thurb.) Rydb. along California State Highway 4 in the vicinity of Lake Alpine, Alpine Co., California (WSP 42875). This is probably the second report of powdery mildew on this grass because the host of a collection from Tuolumne Co., Calif. ("Nev.") (WSP 37378) found in the WSC Phanerogamic Herbarium (**22**, p. 112, tab. 1) is almost certainly also *A. variabilis* rather than *A. rossae* Vasey as originally determined. In Chase's revision of Hitchcock's manual (**5**) *A. rossae* is given as a local species restricted to the Yellowstone Park area, while most of the other collections belong in *A. variabilis* (cf. also **25**, p. 28). *E. graminis* also occurred on *Poa compressa* L. at Francis, Utah, new to the state on this host (WSP 42945).

CLAVICEPS PURPUREA (Fr.) Tul. is common in California on *Elymus*

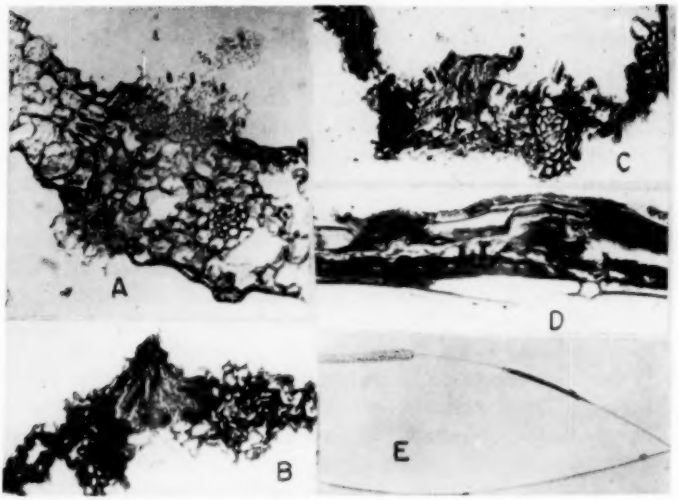


FIG. 2. Photomicrographs. FIG. 2, A. *Colletotrichum sierraensis* from TYPE, showing acervuli. × 175. FIG. 2, B. *Muirella alascensis* from *Elymus glaucus*, Dosewallips R., Wash., showing cross section of developing sporodochium. × 235. FIG. 2, C. Same but slightly more mature. × 155. FIG. 2, D. Same, longitudinal section showing sporodochium. × 157. FIG. 2, E. *Balansia strangulans* on *Phleum pratense*. × ½.

cinereus Scribn. and Merr. (*E. condensatus* Amer. Auct.) but apparently has not been reported (**25**). A collection from Lake Mono, Calif. (WSP 42922) gives a record for California. It should be pointed out that the check list of Sprague and Fischer (**52**) followed the old traditional classification of giant wild-rye and not the revised concept of Chase (**5**). *E. condensatus* Presl is now recognized as a localized relatively gigantic form growing along the California seacoast while the widespread "giant" wild-rye of the arid Far West is now considered *E. cinereus*. Therefore, most of our reports of fungi on *E. condensatus* belong under *E. cinereus*. Except for the report of *Septoria infuscans* (Ell. and Ev.) Sprague from San Diego, Calif., *S. pacifica* Sprague from central California and one or two rust collections, all of the reports in our check list (**25**) will be transferred to *E. cinereus* in a contemplated revised edition.

PHYLLACHORA TEXENSIS Orton occurred on *Muhlenbergia* sp. at Km. 412 Morelia-Guadalajara, Prov. of Jalisco, Mexico (Herb. Cript. 1582). The material was collected by W. D. Yerkes and A. Perez on Aug. 14,

1954. It was very kindly forwarded by Senorita M. Zenteno Zevada, who sent a number of specimens for determination. This first mentioned contains a number of dull black, linear fruiting bodies bearing elliptical ascospores, 13–15 × 6.8–7.3 μ, accompanied by multitudes of curved, filiform spermatia about 10–15 × 0.5 μ. Except for the presence of the spermatia, which Orton does not mention in his original description (**12**), the Jalisco material is readily referable to *P. texensis*. I briefly discussed comparable material several years ago (**19**, p. 568). Ex Herb. Cript. 1582, above cited, has been given our WSP series number 42934. Another specimen on *Muhlenbergia* sp. collected by E. Hernandez in Guanajuato State, Mexico, Sept. 16, 1946, has pip-shaped spores with a slight twist to the narrowed smaller end and up to 17 μ long. The spores have a clear band across their middles which gives them a false-septate appearance. Microspores present are filiform and curved. This fungus is also referred to *P. texensis* (WSP 42944).

PHYLLACHORA GRAMINIS (Pers.) Fckl. occurred on Cynodon sp. at "La Cerona," Chapingo, Mexico, collected Aug. 24, 1946, by J. Rodriguez (Herb. Nac. Mexico). I cannot find any report of *Phyllachora* on *Cynodon* from the western hemisphere. There is a fungus mentioned in the literature called *P. graminis cynodontis* Sacc. and reported as *P. cynodontis* (Sacc.) Niessl later (**15**, v. 2, p. 602). The Mexican material with its narrow asci, 60–80 × 8–9 μ, and small spores seems very similar to *P. graminis*, actually closer to that species than to *P. cynodontis*. It is therefore filed as *P. graminis* (WSP 42936).

DAVISIELLA ELYMINA (Davis) Petrak (WSP 42938) is associated with *Phyllachora* on *Agrostis* sp. collected by E. Hernandez in the State of Oaxaca, Mexico, July 24, 1953.

PHYLLACHORA sp. was found on *Hyparrenia* sp. at Cordoba, Vera Cruz, Mexico, Dec. 30, 1954, by C. Tapia (Herb. Nac. Mexico; WSP 42942). The immature, somewhat interrupted stromata contain masses of tinted, curved, linear spores 13–15 × 0.5 μ. I cannot find any report of a parasitic fungus on *Hyparrenia*. The host is related to *Andropogon* and *Sorghum*. Better material is needed of this fungus.

FUSARIUM AVENACEUM (Fr.) Sacc. caused a brown decay of leafy green tissue of a gall on *Muhlenbergia racemosa* (Michx.) B.S.P. growing in brush in Oak Creek Canyon, Ariz. (WSP 42909). The specimen was sent to W. L. Gordon, who cultured the fungus and very kindly made the determination for the writer. A slide mount of WSP 42909 from the surface of the leafy gall is filed at Washington State College.

FUSARIUM NIVALE (Fr.) Ces. caused a narrow, brown lesion on the sheaths, culms and leaves of living *Festuca viridula* Vasey growing in

alpine meadows in the vicinity of Horsehead Pass, Chelan Mts., in Okanogan and Chelan Counties, Wash., in early August, 1957, (WSP 42864). It is not unusual to find the snow mold fungus attacking plants during the summer under cool wet circumstances.

HELMINTHOSPORIUM SICCANS Drechsl. occurred on *Lolium perenne* L. at Chapingo, Mexico, leg. E. Hernandez, July 12, 1954 (WSP 42940). This fungus was included in the material sent by Martha Zenteno Zevada.

HELMINTHOSPORIUM STENACRUM Drechsl. was present in trace quantities on brown basal leaves of *Agrostis variabilis* Rydb. along the trail to Lower Eagle Lake above Gold Creek, Okanogan County, Washington, August 9, 1957 (WSP 42867). The host is new for this fungus.

A black scurf on the leaves of *Sporobolus cryptandrus* (Torr.) A. Gray was noted in Oak Creek Canyon, Ariz., Sept. 1, 1957 (WSP 42876). The spores measured 30–60 × 10–11 μ, mostly 5-septate, light brown, slightly sigmoid. There is one report of *H. ravenelii* Curt. on *S. cryptandrus* from Wisconsin. This fungus is known, however, largely for its black, smut-like growth on heads of *S. poiretii* (Roem. and Schult.) Hitchc. in the southern states. I sent material to E. S. Luttrell, who suggested that the Arizona collection was not typical of *H. ravenelii*. Until further critical study can be made of this and of a number of other species of *Helminthosporium* on grasses from the Far West we will assign this fungus to H. RAVENELII.

HELMINTHOSPORIUM CYNODONTIS Marig. occurred on *Cynodon dactylon* (L.) Pers. in lawns at Phoenix, Ariz. (WSP 42932), leg. Arda Sprague Rutherford, Aug. 1957.

A fuscous spot on living leaves of *Panicum bulbosum* H.B.K. was found in Oak Creek Canyon, Ariz., Sept. 1, 1957 (WSP 42951). A few spores of *Helminthosporium* sp. were found in the younger lesions. The spores were curved to nearly straight, yellow-brown, 80–110 × 12–14 μ, 5- to 7-septate. On older leaves the lesions were overrun with *Cladosporium* sp., with some spores resembling *Fusicladium*. The cause of the original spot appears to be the *Helminthosporium*. The fungus is close to *H. micropus* Drechsl. Better material is needed for further study. No species of *Helminthosporium* causing a leafspot on *Panicum* is common in the Far West.

OVULARIA PUSILLA (Ung.) Sacc. and D. Sacc. is common on *Festuca arizonica* Vasey in the woods towards the Snow Bowl out of Flagstaff, Ariz. (WSP 42898; 42960). The brown spots on the filiform leaves are small but abundant. The spore production is light, rather typical of the fungus. This is the first report of a parasitic fungus on this local

grass, although the host has been examined carefully many times in earlier and drier years.

RHYNCHOSPORIUM SECALIS (Oud.) J. J. Davis occurred on *Bromus vulgaris* (Hook.) Shear along a fork of Prince Creek near Cub Lake, Chelan Co., Wash. (WSP 42866). The spores are slender, only slightly hooked, therefore close to *R. orthosporum* Cladwell. The record on this host, surprisingly, is new for the western region, at least. *R. secalis* was relatively abundant on, and sometimes destructive to, a number of grasses growing in aspen or mixed woods at about 8,000 feet elevation in the mountains of Utah in early September, 1957. Among unreported hosts from Utah we have *Bromus carinatus* Hook. and Arn., near Monte Cristo Peak (WSP 42880), and *Elymus glaucus* Buckl. in the same area (WSP 42976) and in the Wasatch Natl. Forest, 19 miles east of Kamas, Utah (WSP 42924). Good material was obtained on *Bromus inermis* Leyss six miles west of Navajo Lake on Utah State Highway 14 (WSP 42928). Scald is not common on this economically important host in the West. It has been previously reported once each from California, Oregon and Washington (**25**).

SCOLECOTRICHUM GRAMINIS Fckl. occurred on *Stipa californica* Merr. and Davy at Crater Lake, Oregon, in a dry sandy habitat. The spores were mostly non-septate but a few were fusiform and showed faint beginnings of a cross wall (WSP 42926). The host is newly reported for this fungus. The same fungus was found on *Hordeum brachyantherum* Nevski at Tioga Pass, Calif. (WSP 42956), a new record for the state on this usually common host. In our travels in Arizona we found the fungus scarce in 1957 but a trace was found on *Agropyron smithii* Rydb. in a drying meadow along the road to the Snow Bowl out of Flagstaff, Ariz. (WSP 42888). Even this record was new to Arizona. The same fungus is new to Utah on *Phleum alpinum* L. at the base of Bald Mt. (about 9,000 ft. elevation) and on this host is new to California at Tioga Pass (WSP 46036).

PHYLLOSTICTA SORGHINA Sacc. caused white, red-bordered lesions on *Chloris virgata* Swartz growing in red soil in the desert along U. S. Highway 66 near Pica, northern Yavapai County, Ariz., following heavy rains in late August, 1957. The material (WSP 42970) was scanty, but one distinct lesion bore several prominent, brown pycnidia (75–150 μ diam.) containing hyaline, aseptate spores, 6–7.2 × 2.2–2.8 μ. *Chloris* appears to be a new host-genus for this fungus.

A leafspot on *Muhlenbergia racemosa* growing in brush in Pump House Wash at the head of Oak Creek Canyon, Ariz. (WSP 42908) is tentatively referred to PHYLLOSTICTA MINUTASPORA Sprague (**16, 23**).

The lesions at first appear as fuscous or gray streaks. Later these become pale in the centers, expand to nearly the width of the leaf and develop a narrow, reddish margin. The leaf very often breaks or shreds at these points so that most of the diseased tissue disappears. Pycnidia found were of two kinds; most of them were small (60–90 μ) and contained bacterium-like, non-septate, hyaline spores, 3–6 × 0.5–0.7 μ. *P. minutaspora* has only slightly shorter spores, 3–4 × 0.5–0.7 μ but the symptoms of the type on *M. filiformis* (Thurb.) Rydb. differ from those on *M. racemosa*. The type has symptoms called "yellow leaf" (**18**). However, the difference in symptoms may be due to the considerably more robust host of the Arizona material. This could also account for the slightly larger spores. At least until we obtain further material for comparison, it is conservative to call the Oak Creek material *P. minutaspora*.

In the above discussion mention was made of some larger pycnidia. They contained 7-septate spores of HENDERSONIA CULMICOLA Sacc. (WSP 42907). I have seen many spore mounts of *H. culmicola* during the past 30 years and made numerous camera-lucida drawings but this material differs from all others of *H. culmicola* in being obviously completely mature with well-rounded, 7-septate spores. When left overnight in a water mount these spores started to germinate from their distal cells.

SELENOPHOMA BROMIGENA (Sacc.) Sprague and A. G. Johnson was found in a few spots on leaves of *Bromus ciliatus* L. growing under aspens on the Snow Bowl Road out of Flagstaff, Ariz. (WSP 42929). The spores ranged up to 30 μ long (cf. WSP 20525 from Climax, Colo.). *S. bromigena* has been found on *B. ciliatus* in small quantities in three widely scattered parts of the West. Either the habitat in woodland areas is unfavorable or the host is resistant.

SELENOPHOMA DONACIS (Pass.) Sprague and A. G. Johnson is new to Arizona on *Sporobolus cryptandrus* (Torr.) A. Gray. It was found in Oak Creek Canyon, Ariz., Sept. 1, 1957 (WSP 42903).

SELENOPHOMA EVERHARTII (Sacc. and Syd.) Sprague and A. G. Johnson occurred scantily on culms of *Bouteloua eriopoda* (Torr.) Torr., a new host, at the entrance to Wupatki Natl. Monument on U. S. Highway 89, Arizona, on Sept. 3, 1957 (WSP 42930). The few spores seen were about 10 × 1.2 μ and were borne in very small, scattered pycnidia on dried culms. Except for a very recent heavy rain, the region had been dry for a long period. Other than smuts, this is the first fungus reported on this black grama.

SELENOPHOMA OBTUSA Sprague and A. G. Johnson, a common leafspot on *Elymus glaucus* Buckl., is new to Utah in our lists. It was found

at Mirror Lake in the mountains about 35 miles east of Kamas (WSP 42952). The spores are falcate, in the main, but blunted on the ends, typical of the species.

SEPTORIA AVENAE Frank was abundant on *Glyceria* spp. in swampy areas in Pend Oreille Co., Wash., and in adjacent Bonner Co., Ida., in late June and early July, 1957. One collection on *G. elata* (Nash) Hitchc. from the upper West Branch of the Priest River, Idaho, is new to the state (WSP 42856). *S. avenae* was also collected on *G. elata* along a small creek near Battle Mountain State Park, Oregon (WSP 42985).

Some poor material of a pycnidial form with 3-septate, cylindrical spores 28–35 × 3.0 μ was found on *Bromus ciliatus* L. in Oak Creek Canyon, Ariz., Sept. 3, 1957 (WSP 42957). For the sake of consistency (cf. **24**) we should assign this collection to *Stagonospora bromi* A. L. Sm. and Ramsb., but this particular material is indistinguishable from *Septoria avenae* and is so classified. The pycnidia occur with *Puccinia recondita* Rob. ex Desm. and appear to be secondary to the rust in this instance. Another collection on *B. ciliatus* from Oak Creek Canyon had dark brown lesions as in *St. bromi* and the spores were 1- to 3-septate, 21–25 × 3.0–3.5 μ. This, also, is closer to *Stagonospora bromi* (WSP 46046).

SEPTORIA ELYMI Ell. and Ev. caused a severe stunting on all aboveground parts of *Agropyron trachycaulum* (Lk.) Malte growing along the road to the Snow Bowl area near Humphrey's Peak, Coconino Co., Ariz., Sept. 3, 1957. The writer and Fischer finally decided that the host was *A. trachycaulum*. The diseased heads were thickened, shortened, slightly awned and very brittle, snapping off like celery stalks when bent. A few plants developed short rhizomes where they were growing in duff but most of the plants were closer morphologically to slender wheatgrass than any other species. The spores in this material were 1- to 3-septate, 40–55 × 1.3–2.4 μ, equal in size to *S. elymi* f. *elymina* (Davis) Sprague but with septations typical of the species proper. We have never seen as severe an infection of *S. elymi* as occurred on this host in this location. The area was a grassy, open meadow surrounded by aspens. We also encountered *S. elymi* on *A. smithii* Rydb., near Williams, Ariz. (WSP 46042). The arcuate spores were assigned to f. *elymina* because of their larger size.

Several years ago I reported atypical material of SEPTORIA INFUSCANS (Ell. and Ev.) Sprague on *Elymus canadensis* L. collected near Cimmarron, New Mexico (**18**; pp. 560–561). I have the same kind of

material on the same host collected in a brushy area in Pump House Wash in the Oak Creek Canyon, Ariz. (WSP 42898) on Sept. 1, 1957. The lesions, when young, were fuscous but later faded to gray or tawny, vein-delimited streaks. The pycnidia are 70–80 × 70–110 μ with a tendency towards an elliptical outline. The spores are atypical, somewhat curved, pointed at the ends, 1-septate, rarely 3-septate, 13–28 × 2.0–2.6 μ (Fig. 1, B). Some secondary spores were formed by germination. The fungus was associated in part with *Hendersonia culmicola* Sacc. (WSP 42897) and *H. crastophila* Sacc. (WSP 42899).

In addition to *Septoria avenae* associated with leaf rust on *Bromus ciliatus* in Oak Creek Canyon, I encountered material of *S. nodorum* Berk. on the same host in the Pump House Wash fork of the Canyon (WSP 42885). This is comparable to some material reported from New Mexico several years ago (**19**).

SEPTORIA OUDEMANSII Sacc., found on *Poa pratensis* L. in Oak Creek Canyon, Ariz., Sept. 1, 1957, is unreported from this state.

SEPTORIA PASSERINII Sacc. developed microspores on *Sitanion hystrix* (Nutt.) J. G. Sm. in Oak Creek Canyon, Ariz. The numerous pycnidia contain straight to comma-shaped spores, 4–7 × 0.4–0.7 μ (cf. **18**, p. 250, *fig. 44, A* and *44, D*).

SEPTORIA POLIOMELA Sydow, found on *Deschampsia elongata* (Hook.) Munro along the highway at the top of Whitebird Grade, near Grangeville, Idaho (WSP 42884), is newly reported for Idaho.

An abundance of dark brown spots on leaves of *Oryzopsis micrantha* (Trin. and Rupr.) Thurb. occurred in the shade of limestone cliffs in Lee's Canyon, Nevada. Most of the material is immature but a few lesions bore pycnidia containing a few one-septate spores of STAGONOSPORA SIMPLICIOR Sacc. and Berl. (WSP 42868). The *Ascochyta* phase has typical blunt spores, 16–24 × 9–11 μ. Some of the spores are *Apiocarpella*-like. The mature lesions are elongate and white with strongly contrasting brown borders. The much more common immature ones are rectangular to elongate and brown throughout. The summer stage of *St. simplicior* has been discussed previously, especially in relation to its occurrence on *Stipa* (**1**). The fungus had been found previously on the hybrid *Stiporyzopsis* but not on *Oryzopsis* itself. *St. simplicior* was also found on its common host, *Stipa lettermani* Vasey, near Navajo Lake, Utah, and is unreported from the state (WSP 42913). It was also collected on this host 24 miles east of Huntsville, Utah, toward Monte Cristo Peak (WSP 42915).

STAGONOSPORA VEXATULA Sacc. occurred on dying leaves of *Des-*

champsia elongata (Hook.) Munro ex Benth. in the Wasatch Natl. Forest, about 19 miles east of Kamas, Utah (WSP 42948). The fungus is similar to material found on *D. caespitosa* (L.) Beauv. (**25**). The fungus may be weakly parasitic.

SYNCHYTRIUM GRAMINICOLA Sprague caused black elliptical lesions on basal leaves of *Poa reflexa* Vasey and Scribn. at the foot of Bald Mountain about 30 miles east of Kamas, Utah (WSP 42953). The elevation was approximately 10,000 feet in a rocky, meadow-like area. When examining this in the field, the writer assumed from the appearance of the lesions that the fungus was possibly *Entyloma dactylidis* (Pass.) Cif. or *E. spragueanum* Zundel. However, microscopic examination revealed a few closely grouped, amber-colored sori in the center of the spots. The sori were 70–128 × 90–140 μ. These are assigned to *S. graminicola*, but with some hesitation.

GLOEOCERCOSPORA ALASCENSIS Sprague was described as having *Titaeospora*-like paired spores (**20**). I have had opportunity to study many prepared slides made by Mrs. Peggybeth Figaro from the type and from a collection from the state of Washington (WSP 37466). The fungus forms a deep-seated, sporodochium-like mass (FIG. 2, B) and penetrates laterally and particularly vertically, pushing through to the surface. Sometimes, as shown by longitudinal sections, it spreads for some distance along the leaf surface. The fungus, therefore, appears from the surface as a moniliaceous form but shows definite melanconiaceous eruption of the tissue in cross section. It is, however, certainly closer to the Tuberculariaceae. The fungus resembles *Ramulispora sorghi* (Ell. and Ev.) Olive and Lefebvre (**11**) but the spores, like those of *Titaeospora*, are united in pairs at their base, not branched as in *Ramulispora*. Its tendency to spill out over the leaf in pustules is like *Gloeocercospora*. The fused spores plus the now evident deep-seated nature of the fruiting body would exclude the fungus from *Gloeocercospora* and the presence of fused spores eliminates *Ramulispora*. If we were to accept this as an acervulus form, it could be transferred to *Titaeospora*. However, the mature surface extends as much as 28 μ above the leaf surface and farther along the surface. Hence, the fruiting structures are true sporodochia when mature and belong to the Tuberculariaceae. Some have placed this family in the Melanconiales, and, in our case, with reason. Since *Titaeospora* produces a true acervulus (cf. **11**) we cannot assign our fungus to that genus. This leaves our fungus without an assignable, described genus. I therefore propose:

MUIRELLA gen. nov.

Maculis in foliis vivis, sporodochiis erumpentibus, albidis, hyphis hyalinis, septatis; conidiophoris tenuibus, sublinearibus; sporulis hyalinis v. dilute chlorinis, cylindraceo-fusiformibus, prope basim in paribus unitis, 1–3-septatis.

TYPUS est **Muirella alascensis** (Sprague) comb. nov. (*Glococercospora alascensis* Sprague, Mycologia **46**: 76. 1954.)

Spots in living leaves; sporodochia erumpent, white; hyphae hyaline, septate; conidiophores delicate, sub-linear; spores hyaline to faintly tinted, cylindrical-fusiform, fused in pairs near their bases, 1- to 3-septate.

The genus is dedicated to the late John Muir, naturalist, near whose cabin-site at Glacier Bay, Alaska, this fungus was first found on *Trisetum spicatum* (L.) Richt. The later material, which is better than the type, was collected on *Elymus glaucus* along the Dosewallips River in the Olympic Mts., Wash. (WSP 37466).

A key to distinguish this group of genera follows:

A. Spores produced on sporodochial pads
  1. Spores branched.....*Ramulispora*
  2. Spores single.....*Glococercospora*
  3. Spores fused at base in pairs.....*Muirella*
AA. Spores produced in acervuli.....*Titacospora*

What I must call SEPTOGLOEUM OXYSPORUM Sacc. Bomm. and Rouss. occurs scatteringly on *Glyceria* spp. in the western states. I have some material on *G. grandis* S. Wats. found growing in running water and at streamside near Aspen Mirror Lake about 28 miles east of Cedar City, Utah. The char spot causes a black stem or sheath condition often at the surface of the water. There are a few nearly mature lesions which have the typical off-white or pale buff mass of spores surrounded by the black stomatic area (WSP 42978). Most of the spores are just beginning to form one nearly-central septum, although a considerable number are non-septate. The slightly curved spores are much larger at one end than the other. They measured 19–21 × 4.5–5.8 μ in one mount and 19–25(–28) × 4.5–5.6 μ in another. I saw one spore which showed evidence of becoming tri-septate. I could find no setae as in *Colletotrichum aquatilis* Sprague (**24**) nor has this particular fungus ever shown any of the black char symptoms. The Utah fungus has smaller spores than *C. aquatilis* but the spores are certainly very similar in appearance. As I have indicated earlier, the complex known as *S. oxysporum* needs host-range study before it can be satisfactorily cleared (**18**).

I also have some char spot material on *Glyceria grandis* from a

marshy area 17 miles east of Huntsville, Utah (WSP 46028). There are a few spores of *Septogloeum* present that measure 23–30 × 4–6 μ. The most abundant fungus present is a developing perithecial form. The globose fruiting bodies are strongly erumpent, almost superficial, black, 140–200 μ with a small apical pore 12 μ in diameter. The stroma, if it can be termed such, is a loose web of dark brown mycelium growing sub-superficially between the distinct perithecia. Primordia of asci are well formed and a few asci can be distinguished. They are clavate, 37–70 μ long. Various scattered spore forms are present on the spots, especially *Fusarium* spp., but no spores sufficiently mature to recognize were found in the perithecia. The fungus is distinct from *Dothidella*, possibly nearer to *Physalospora*. It will be necessary to gather material of this fungus in the very late fall in the hopes that mature material will be found. Pure culture work is needed, as well.

In addition to the char spot collections discussed above, I found additional material at Butch Creek, Pend Oreille Co., Wash., July 15, 1957, on *Glyceria pauciflora* Presl (WSP 46038). Spores were 21–28 × 4.3–5.8 μ. A few very young perithecial fruiting bodies comparable to those in the Utah collection (WSP 46028) were present.

A stem speckle found on *Poa pratensis* L., at the Klamath County line, south of Lapine, Oregon, belongs under SELENOPHOMA DONACIS (Pass.) Sprague and A. G. Johnson rather than the var. *stomaticola* which is commoner on *P. pratensis*. The spores are mostly boomerang shaped, 15–21 × 2.4–2.8 μ (WSP 42982).

DILOPHOSPORA ALOPECURI (Fr.) Fr. was prevalent on *Agropyron trachycaulum* at about 9,100 ft. on Monte Cristo Peak, Utah (WSP 42987).

RHYNCHOSPORIUM ORTHOSPORUM Caldwell was abundant in swampy areas near Kamas, Utah, on *Calamagrostis canadensis* (Michx.) Beauv. (WSP 42994).

STAGONOSPORA MARIAE Sprague was found on dark, dead leaves of *Agrostis alba* L. along an irrigation ditch at Huntsville, Utah (WSP 42996). All of the previous material has been found along the seacoast (**24**). I assigned the material from Huntsville to this species only after detailed study and then with considerable doubts as to its identity. The spores of the Utah specimen are greenish, cylindrical, somewhat pointed at the apex, blunted at the base, sometimes constricted at the 3 to 7 septa, 49–70 × 4.2–5.3 μ, borne in light brown to brown pycnidia, 85–145 μ diam. This fits the description of *St. mariae* except that the spores are greenish, not hyaline. They tend to be straighter than spores from the type of *St. mariae* and they give the impression of belonging closer

to *Septoria* than the slightly coarser spores of the type. I recently concluded that *St. mariae* differed from the complex of forms that Webster (**27**) related to several species of *Leptosphaeria* (**23**). On the basis of a number of earlier studies (**18**) such fungi as *Septoria alopecuri* (Karst.) Sydow, *S. epigejos* v. Thum., *S. rhizodes* Bres. and Krieg., *Hendersonia crastophila* Sacc. and *Stagonospora arenaria* Sacc. would also have to be eliminated. The spores of *Stagonospora intermixta* (Cooke) Sacc. appear to be smaller than those of the Utah fungus. The Utah fungus is therefore assigned for convenience to *St. mariae*, its closest relation.

After working with some 150 isolations of *Wojnowicia graminis* (McAlp.) Sacc. and D. Sacc. I concluded that it was very difficult to segregate this fungus from an intergrading form that is known generally as *Hendersonia crastophila* Sacc. (**18**). I therefore lumped the group under *H. crastophila*. Some years since then Webster, in detailed work, showed that the conidial stage of *Pleospora vagans* Niessl was a *Hendersonia* which, I would agree, is my concept of *H. crastophila* based on the original description (**27**). However, Webster pointed out that neither he nor I ever found an ascigerous stage connected with *Wojnowicia graminis* sensu stricto. It is apparent that this is another case of two similar pycnidial stages which are not related. It is, therefore, necessary to recognize *W. graminis* as separate from the pycnidial stage of *Pleospora vagans*. *W. graminis* tends to produce spores which are somewhat flattened on one side and somewhat more falcate than fusiform. I prefer to consider this fungus a good species of *Hendersonia*, using the older name of H. GRAMINIS McAlp. *H. graminis* seems to be an earlier invader of tissue than *P. vagans*. It is the common species in wheatlands in the semi-arid west (**18**).

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STUDIES ON PTYCHOGASTER RUBESCENS BOUD. THE CHLAMYDOSPORIFEROUS FORM OF POLYPOROUS GUTTULATUS PK.[1]

OSWALDO FIDALGO[2]

(WITH 4 FIGURES)

Corda (**1837**) described the genus *Ceriomyces* for one species, *C. Fischeri*. Later (**1838**) he characterized a similar additional genus, which he named *Ptychogaster*.

Fries (**1849**, p. 315) indicated that "*Ceriomyces* Corda est status degener *Daedaleae*," and in the same work (p. 564) noted that *Ptychogaster* "est nempe monstrosa progenies *Polypori borealis*, his diebus a me plene observata."

Boudier (**1887**) described two new species of *Ptychogaster* from Montmorency (France), one of them called *P. rubescens*. Concerning this species he wrote (p. 11), "Le développement de cette espèce parmi le *Polyporus vaporarius* fréquent dans les serres me la fait regarder comme l'état conidiophore de ce champignon, bien que je ne puisse le certifier d'une manière absolue." Saccardo (**1888**) transferred *P. rubescens* to *Ceriomyces*. Later Brefeld (**1889**) included it in *Oligoporus*.

According to Bresadola (**1903**), *P. rubescens* was connected with *Radulum spathulatum* (Schrad.) Bres. by Hennings. The author has been unable to verify this reference; instead, in three different papers, Hennings cites Boudier's surmise as a basis for recognizing the possibility of such a connection. Killermann (**1922**, p. 102) found *P. rubescens* to be a form of *Polyporus borealis* Fr. Later Davidson, Christensen and Darley (**1946**) examined a culture of *P. rubescens* from Baarn (Holland) and found it to be very close to cultures of *Polyporus guttulatus* Pk. Subsequent studies show great similarity between these cultures.

[1] This work was done with the assistance of a grant-in-aid from the National Council of Research of Brazil. The author is happy to acknowledge the use of the facilities of the National Fungus Collections, U. S. Dept. of Agriculture.

[2] Instrutor of the Faculdade Nacional de Filosofia da Universidade do Brasil and Naturalista of the Jardim Botanico do Rio de Janeiro, Distr. Fed., Brasil.

I obtained the type of *P. rubescens* from Paris and compared it with cultures of this and all other fungi suspected in connection with this chlamydosporiferous form.

PTYCHOGASTER RUBESCENS Boud., Jour. de Bot. **1**: 10–12. *t. 1, fig. 2.* 1887.

Synonymy: *Ceriomyces rubescens* (Boud.) Sacc., Syll. Fung. **6**: 387. 1888. *Oligoporus rubescens* (Boud.) Bref., Unters. **8**: 136. *t. 8, 42–43.* 1889.

The type is represented by two pieces, Blackish Brown (*2*) (Ridgway, *pl. XLV*), 1.5 × 1.3 cm and 1.8 × 1.1 cm. Microscopic examination shows the presence of generative hyphae which are hyaline, thin-walled, colorless, with granular contents and abundant clamp-connections, 2.5–3.5 μ in diameter. The chlamydospores are elliptic, subglobose to globose, at first hyaline, colorless, but later with granular contents and not so transparent, with a pinkish color, 5.5–7.5 × 3–5 μ (Boudier gave 5–7 × 4–5 μ).

Davidson sent to me the same culture from Holland that he used as the basis of his work (**1946**). TABLE I shows the similarity between the cultural and the type characters of *P. rubescens*. On the basis of this comparison, it seems to us that both, type and culture, belong to the same species.

About the supposed connection of *P. rubescens* with the four species of hymenomycetes indicated in TABLE I, we can see that on present information only *Polyporus guttulatus* could be the normal form of *Ptychogaster rubescens,* because cultures of the two present practically the same color, the same kind of hyphae, and chlamydospores of the same color, shape and size.

Polyporus borealis also produces chlamydospores in culture but these are very different in color and size. In cultures of *Radulum spathulatum* and *Poria vaporaria* I was unable to find chlamydospores.

MATERIAL EXAMINED

Specimen: TYPE of *Ptychogaster rubescens,* Montmorency, France, "ad lignum fabrefactum in caldario," Jan. 1885.

Cultures: *Ptychogaster rubescens,* Centraalbureau voor Schimmelcultures; 94372, rot isolate, pine joists, house in Alexandria, Va., coll. *J. D. Diller,* isol. and det. R. W. Davidson, Aug. 24, 1948.

Polyporus guttulatus, 71799, sporophore tissue isolate, balsalm

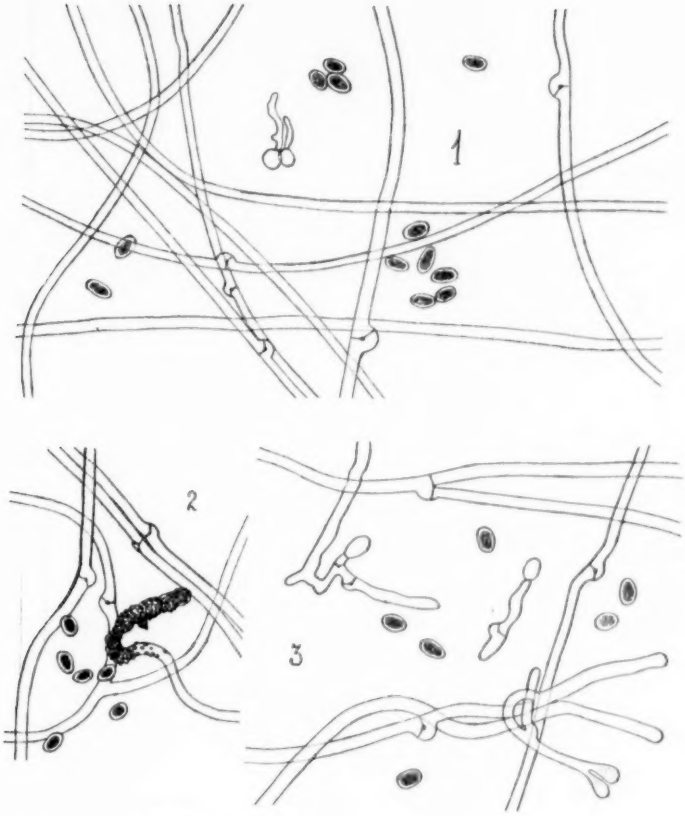

FIG. 1. Drawn from culture of *Ptychogaster rubescens.*

FIG. 2. Structural elements of the type of *Ptychogaster rubescens.*

FIG. 3. From culture of *Polyporus guttulatus:* chlamydospore, chlamydospore germinating, chlamydospore formation, hyphal tips covered with crystals. × 1130.

fir, Itasca Park, Minnesota, coll. *Clyde M. Christensen,* Aug. 20, 1937.

Polyporus borealis, 71204, sporophore tissue isolate, hemlock, Tionesta National Area, Pa., coll. L. O. Overholts, W. A. Campbell and Bailey Sleeth, Aug. 14, 1936; 91430, sporophore tissue isolate, sitka spruce, decay of heartwood at base of living tree, Long Island,

TABLE 1

COMPARISON OF PTYCHOGASTER RUBESCENS AND CULTURES OF FOUR HYMENOMYCETES

	TYPE	CULTURES				
SPECIES	*Pt. rubescens*	*Pt. rubescens*	*Pol. guttulatus*	*Pol. borealis*	*R. spathulatum*	*P. vaillantii* (=*P. vaporaria*)
COLOR	Blackish Brown (2)	Vinaceous-Buff to Cinnamon-Drab	Light Vinaceous-Fawn to Fawn Color	White to Cream Color	White to whitish	Pure white
HYPHAE:	Generative, hyaline with granular contents	Generative, hyaline with granular contents	Generative, hyaline with granular contents	Generative, hyaline with granular contents	Generative, hyaline with granular contents	Generative, hyaline without granular contents
Diameter	2.5–3.5μ	1.5–3.5μ	2.5–4μ	2–8μ	2.5–4μ	1.5–5.5μ
Clamp-connections	Present	Present	Present	Present	Present	Present
Simple cross walls	Not present	Not present	Not present	Not present	Not present	Not present
CHLAMYDOSPORES	Present	Present	Present	Present	Not observed	Not observed
Color	Dark pink	Light pink	Light pink	Colorless	—	—
Shape	Ellipsoid, subglobose to globose	Ellipsoid, subglobose to globose	Cylindric, ellipsoid, subglobose to globose	Ellipsoid, subglobose to globose	—	—
Size	5.5–7.5×3–5μ	5.5–7.5×3–5μ	5–8×2.5–5μ	9.5–19.5×7–12.5μ	—	—
HYPHAL TIPS COVERED WITH CRYSTALS	Present	Not observed	Not observed	Present	Not observed	Not observed

FIG. 4. Type of *Ptychogaster rubescens*.

Tongass Natl. Forest, Alaska, coll. G. H. Englerth, det. L. O. Overholts, Oct. 2, 1942.

Radulum spathulatum, 94484, polysporous isolate, fruiting on wood (part of understructure) of house in Washington, D. C.; coll. J. D. Diller, isolated by R. W. Davidson and det. by P. L. Lentz, Nov. 23, 1945.

Poria vaporaria, Centraalbureau voor Schimmelscultures (considered to be *P. vaillantii*).

CONCLUSION

It seems to me that *Ptychogaster rubescens* Boud. is really the chlamydosporiferous form of *Polyporus guttulatus* Pk. as suggested by Davidson, Christensen and Darley (**1946**) and has no relation with *Polyporus borealis, Radulum spathulatum* or *Poria vaporaria*.

ACKNOWLEDGMENTS

To Ross W. Davidson, Hazel M. McKay and Frances F. Lombard we are indebted for the cultures and information given.

RESUMO

Ptychogaster rubescens Boud. tem sido indicado como forma clamidosporífera de diferentes espécies. Foi nosso propósito comparar o tipo de *P. rubescens* com culturas desta espécie e de outros fungos citados como formas normais de *P. rubescens.* Pudemos assim concluir que as culturas usadas por Davidson, Christensen e Darley (**1946**), correspondiam, realmente, à espécie em questão e que *Polyporus guttulatus* Pk. deve ser sua forma basidifera. Qualquer possibilidade de conexão desta forma com *Polyporus borealis, Radulum spathulatum* ou *Poria vaporaria* é excluida.

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MECHANISM OF APOTHECIAL OPENING AND ASCOSPORE EXPULSION BY THE CUP-FUNGUS URNULA CRATERIUM

FREDERICK A. WOLF

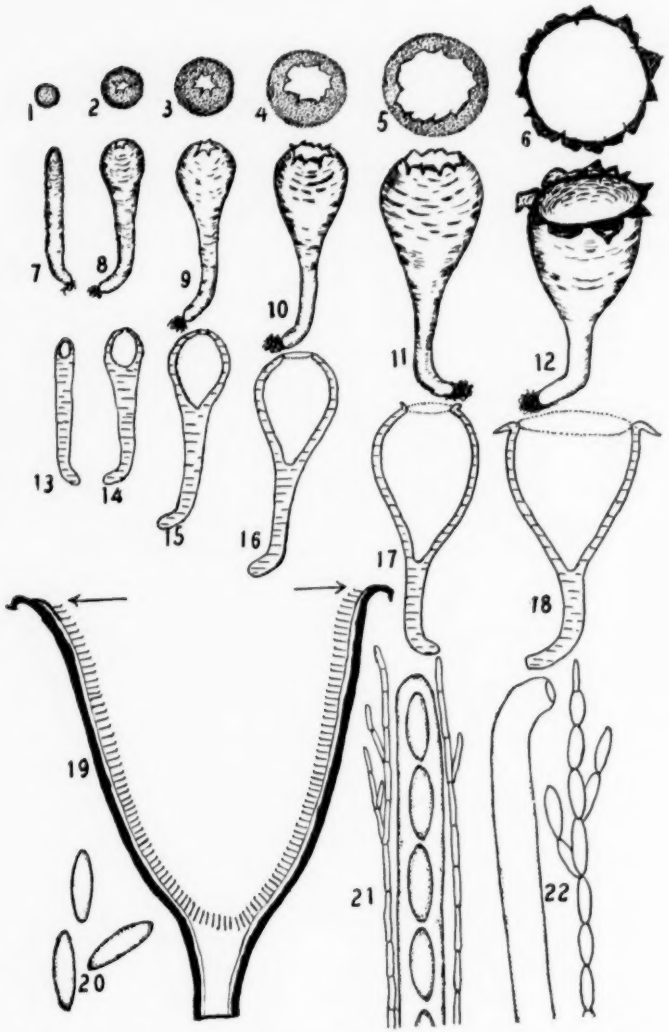
(WITH 23 FIGURES)

INTRODUCTION

The cup-fungus *Urnula craterium* (Schw.) Fries occurs widely throughout the eastern United States. It was first described from North Carolina as *Peziza craterium* (Schr. Nat. Ges. Leipzig **1**: 117. 1822) by de Schweinitz. More than 100 years ago, Fries (Nova Acta. R. Soc. Sci. Upsal. III **1**: 122. 1851) changed the name of this cup-fungus to *Urnula craterium;* he had already (Summ. Veg. Scand. **2**: 364. 1849) made it the generic type. During the period of 140 years that have elapsed since this organism was first described many persons have collected it, but apparently no one has given especial consideration to its structure and development. The present purpose therefore, is to report my observations on its structure and to interpret them in so far as these findings aid in explaining how the apothecia open and how the ascospores are expelled.

APOTHECIAL STRUCTURE

Decaying oak branches, lying on the forest floor, especially when partly buried in the soil or leaf litter, constitute the natural substratum for the growth of *Urnula craterium* and for production of its apothecia. During late autumn the surfaces of such branches that are in contact with the ground may be found to be covered with a dense, black, mycelial weft that extends into the soil and litter and binds all of them together. At this time leathery, black, cylindric stromata, one or more centimeters in length and 3 to 4 millimeters in diameter, will be noted to have arisen from the copious mycelial weft. They stand quite closely applied to the decaying branches. These stromata enlarge slowly throughout the winter. With the advent of warm weather in late March and early April, however, they rather rapidly become transformed into brownish-black, goblet-shaped apothecia (FIG. 23). These changes, stepwise, are



FIGS. 1–18. Three series of comparable sketches of apothecia of *Urnula craterium*. FIGS. 1–6. A series of sketches of the apices of apothecia as seen from above, showing relative diameter and accompanying apertures. FIGS. 7–12. Sketches of entire apothecia, as seen laterally. FIGS. 13–18. Sketches of apothecia, split lengthwise, to show the relative extent of the hymenium. FIG. 19. Diagram

shown by three series of comparable sketches, FIGS. 1–6, representing apothecia as seen from above, FIGS. 7–12, as seen from the side, and FIGS. 13–18, as seen laterally, when the apothecia are split open. It will be apparent that the hymenium arises in the apical region of the cylindric stroma, appearing first as a small cavity. Hymenial development proceeds basipetally, i.e. toward the bottom of the cup. Concurrently with such development, the upper part of the stroma expands and a star-shaped aperture appears at the tip. As the apothecium expands the tissues surrounding the aperture and forming the rim of the cup become jagged, torn, flaccid flaps (FIGS. 12, 23). Oftentimes too the rim is fissured. When fully opened the cups have a diameter of 3–4 cm and a depth of 4–6 cm. The pedicel or stipe is 3–6 cm long and has a diameter of 4–8 mm.

The apothecial wall, if examined microscopically, consists of several layers (FIG. 10). The outer surface is clothed with brownish black tomentum. On scraping off this tomentum there is found a layer of non-elastic, leathery, compact tissue that constitutes approximately one-third the thickness of the wall. This layer is coal black. Inwardly beneath this leathery layer, is a medullary one of approximately equal thickness that is almost colorless. It consists of loosely interlaced slightly brownish hyphae that are embedded in a gelatinous matrix. Immediately beyond this colorless layer is the hymenium. Its surface is brownish-black, slightly paler than the outer surface of the apothecia. The asci are long cylindric, tapering gradually below, and measuring approximately 600×15–$17\ \mu$. Each ascus is provided with a flip-top lid. The nearly colorless ellipsoidal ascospores (FIG. 20) are uniseriate and occupy the upper half of the ascus. They range in size from 25–35×12–$14\ \mu$. Interspersed among the asci are filiform septate, branched paraphyses, that extend beyond the apices of the asci.

MECHANISMS

Microscopic examination of the tissues immediately surrounding the apothecial apertures, beginning when the first fissures appear, reveals that the asci are empty and collapsed and that the paraphyses, except for the tip cells, have changed from branched filaments to chains of

of an open apothecium, showing the outer black leathery wall, the medullary layer, and the hymenial layer. The arrows indicate that pressure is exerted in a horizontal plane in all directions toward the rim. FIG. 20. Ascospores. FIG. 21. Tip of ascus and filamentous paraphyses. FIG. 22. Upper end of an empty operculate ascus, showing phototrophic curvature of the apex, and a paraphysis having ellipsoid cells, except for the tip cell.

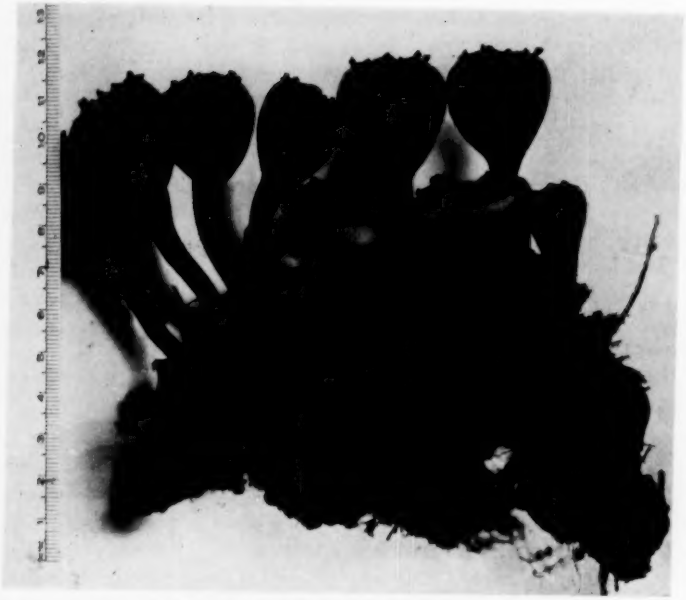


FIG. 23. A cluster of apothecia of *Urnula craterium* seated upon a mass of soil. Note the character of the rim.

ellipsoidal cells. Their diameter (width) is approximately three times that of paraphyses in the hymenial tissue a short distance below the rim of the cup. This zone of collapsing asci and inflated paraphyses is a zone of disintegration that advances downward toward the bottom of the cup. Advance of this zone of disintegration ceases only when the apothecia are fully expanded. By this time all remaining asci and ascospores are mature and the interspersed paraphyses function only to separate the asci. The tips of all asci in an advancing zone just below the rim are curved vertically toward the apothecial opening, a phototropic response to incident light. Such asci elongate to extend beyond the tips of the paraphyses. By the time that the apothecia are fully open the apices of all remaining asci that line the sides and bottom of the cup are directed vertically upward.

Several things must be borne in mind to understand the operation of the mechanisms involved in the opening of the apothecia to expose the hymenial layer, and to provide for the expulsion of the ascospores. First of all, the sequential changes shown in the three series of sketches,

FIGS. 1–18, do not appear to involve the formation of new cells but the expansion of cells such as are already present at the stage represented by FIGS. 1, 7, and 13. Moreover, the outer black wall is tough and leathery; hence it resists pressure applied outwardly in a horizontal plane against the expansion of the apothecium. Also contrary to expectation, the oldest part of the hymenium is nearest the apex of the stroma and the youngest part is that at the bottom of the cup.

The fissuring of the apex of the stroma and subsequent widening of the aperture become primarily a response to the pressure exerted by the swollen or inflated paraphyses. Those that line the orifice must also compress the nearby asci, aiding in expulsion of the ascospores.

The transformation of filamentous paraphyses into chains of bead-like cells is the result of glycolysis of glycogen stored in the hymenium. It was demonstrated by use of Benedict's reagent that glycolysis takes place. Tissues from the cup rim were found to contain reducing sugar, presumably glucose, copper oxide being formed in this reagent, whereas remote hymenial tissues showed the absence of reducing sugar. The medullary layer could have served to supply water for glycolyses, although its primary function appears to be to serve in maintaining turgor of apothecia.

The initiation of activity by the glycolytic enzyme system appeared to be triggered by temperature. This conclusion is partly conjectural but finds a measure of support from observation and experiment. In the first place the apothecia open only with the advent of warm weather. Next, account may be taken of the fact that the leathery outer part of the apothecial wall is black and by virtue of its blackness, during sunny weather, could cause the temperature within the developing hymenial cavity to become elevated to the point that is optimum for glycolysis. Since melanin is a well-known black pigment of common occurrence among fungi, the apothecial tissues of *Urnula craterium* were tested for the presence of this pigment, using concentrated acetic acid as the reagent. As a result of this test the characteristic green color, indicative of melanin, developed in the resultant solution.

DISCUSSION

In 1937, Seaver (**1937**, vide p. 62) noted that the paraphyses of *Urnula Geaster* Peck consist of globose, catenulate cells which function as an ingenious device in the expansion of the hymenium and placement of the asci in such position that the ascospores may be freely discharged. Subsequently, Seaver (**1942**, vide p. 324) commenting on a study of *U. Geaster* by Heald and Wolf (**1910**) stated, "I notice that they have

described the paraphyses as being slender and uniform in thickness throughout their entire length. . . . Since they must have worked with fresh material I do not understand how they could have made such a record." He further states that "The peculiar moniliform or catenulate formation of the paraphyses in this species is absolutely unique in the cup-fungi, so far as the writer's observations have gone."

From the present observations it is established that *Urnula craterium* has bead-like paraphyses like those of *U. Geaster.* Moreover it becomes highly probable that *U. Geaster,* like *U. craterium,* also has paraphyses that remain filiform. In both species the monilioid paraphyses function primarily in the opening, splitting, and expansion of the apothecia, secondarily in expulsion of ascospores, and the paraphyses that remain filamentous function only in the conventional manner.

In the light of findings with these two species of *Urnula* it becomes of interest to learn if other genera of large leathery cup-fungi possess a similar mechanism for apothecial expansion and spore expulsion or whether this mechanism remains unique among species of *Urnula.* It may also be pointed out that more should be learned about the responses of *Urnula* to light, darkness, and temperature. This genus appears to constitute favorable material for evaluation of responses to these environmental factors. Moreover, the pathway of transformation of glycogen to glucose should be elucidated. The course of glycolysis in animals is well known but is very complicated, as shown by a voluminous literature (Heilbrunn, **1955**).

This study emphasizes the too-little-appreciated fact that even "lower forms" exhibit remarkable unity and coordination, involving all constituent parts, as regards structure and function. The control mechanisms that make possible such developmental and functional co-ordination remain essentially unknown.

SUMMARY

The apothecial wall of the cup-fungus *Urnula craterium* consists of three layers, an outer black, non-elastic, leathery one, a nearly colorless, gelatinous, water-holding, medullary one, and an inner brown hymenial one.

The apothecia open as the result of pressure exerted by the paraphyses, which on swelling are changed from branched septate filaments to bead-like chains of ellipsoidal cells. This change is confined to a zone at the rim. Swelling results from increase in osmotic concentration, a consequence of the transformation of reserve glycogen in the hymenial layer to reducing sugar. Apparently melanin in the outer apothecial

wall functions to absorb heat to the extent of initiating the activity of the glycolytic enzyme system. Essential moisture is supplied by the medullary layer.

The apices of the asci are turned upward, a phototropic response.

This mechanism for opening the cup to expose the hymenium is presently known to occur only in *Urnula craterium* and *U. Geaster*.

Addendum—Mycelial cultures of *Urnula craterium* originating from ascospores were planted on decaying branches of oak that had been sterilized. After approximately 6 months, black heaps of conidia had formed. This conidial stage appears to be *Strumella corynoidea* Sacc. and Wint., which Davidson (Mycologia **42**: 735–742. 1950) suspected of being the conidial stage of *Urnula craterium*.

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THE HYPHOMYCETOUS GENERA OF H. W. HARKNESS AND THE ASCOMYCETOUS GENUS CLEISTOSOMA HARKN.[1]

CHESTER A. PEEK AND W. G. SOLHEIM[2]

(WITH 7 FIGURES)

Many of the earlier descriptions of the genera and other taxa of the fungi were so meager as to give no adequate concept of the entities entailed. Critical studies of the types of these taxa are, therefore, needed to determine exactly what each represents. This paper reports a study of the type species of four genera of Hyphomycetes and one ascomycetous genus described by Dr. H. W. Harkness (**7**, **8**) in 1884 and 1885.

It has generally been thought that the Harkness types were destroyed at the time of the San Francisco earthquake and fire in 1906. Thanks to the thoughtfulness and efforts of the late Dr. Alice Eastwood, most of the types, then located at the California Academy of Sciences in downtown San Francisco, were saved and are now housed in the Herbarium in Golden Gate Park. Grateful acknowledgment is made to J. T. Howell of the California Academy of Sciences, Dr. D. P. Rogers, recently of the New York Botanical Garden, and Dr. C. T. Rogerson of the New York Botanical Garden, for the loan of the types of the species studied.

CAMPOSPORIUM

CAMPOSPORIUM Harkn., Bull. Calif. Acad. Sci. **1**: 37. 1884; Kellerman, Jour. Mycol. **1**: 29. 1885; Saccardo, Syll. Fung. **4**: 482. 1886; Lindau, in Engler and Prantl, Nat. Pflanzenfam. **1:1****: 480. 1900; Hughes, Mycol. Papers, Commonwealth Mycol. Inst. **36**: 3. 1951.

[1] Contribution from the Department of Botany and The Rocky Mountain Herbarium of the University of Wyoming, No. 234. Based in part on a thesis submitted by the senior author in partial fulfillment of the requirements for the degree of Master of Science, University of Wyoming.

[2] The work on which this paper is based has been completed by the junior author while on leave at the National Fungus Collections, Beltsville, Maryland. Grateful acknowledgment is made to John A. Stevenson, Curator of the Collections, and his staff for the many courtesies extended during the year. Acknowledgment is also made to the Research Council of the University of Wyoming for a grant-in-aid.

The type species is *Camposporium antennatum* Harkn., Bull. Calif. Acad. Sci. **1**: 37. 1884; Kellerman, Jour. Mycol. **1**: 29. 1885; Saccardo, Syll. Fung. **4**: 482. 1886; Hughes, Mycol. Papers, Commonwealth Mycol. Inst. **36**: 3. 1951. FIGS. 3–4.

The Harkness descriptions of the genus and species follow:

"(*Etym. Campe:* larva, from the resemblance of the spores to the larva of Danais Archippus.)

"Hypha brown, flexuous, septate. Spores 1–2, attached by slender pedicels to the angles of the apex, transversely pluriseptate with filiform setae springing from the apex.

"*Camposporium antennatum.*

"Hypha septate, flexuous, brown, spores 1–2, cylindrical, pale olive-brown, 7–13-septate, attached to the apical angles of the hypha by filiform spiral pedicels; ultimate cells hyaline, the upper one bearing 2, sometimes 1 or 3, filiform setae $\frac{1}{4}$–$\frac{1}{2}$ as long as the spore. μ 70–94 × 10.

"On decaying bark of Eucalyptus globulus. San Francisco, Dec. . . . 2349."

The description given below is based on a study of a part of the type collection.

CAMPOSPORIUM ANTENNATUM Harkn. FIG. 1.

Reproductive structures forming dense olive-brown patches on the surface of the substrate; mycelium penetrating the substrate, rather sparse, hyphae regular to irregular, branched, septate, light brown to dark brown but lighter in color than the conidiophores, about 3.5–7 μ in diam.; conidiophores aggregated to diffuse, erect to ascending, straight or irregularly contorted, dark brown, 48–160 × 6–9 μ, up to 12-septate, tapering rather abruptly at the apex to about 2 μ from which point is developed a hyaline, straight to somewhat spiral or coiled stalk, the separating cell, which is about 4–6 × 2 μ, stalk scars occasionally laterally displaced and shouldered, wall about 1–1.3 μ thick; conidia cylindrical, 45–70 × 7.5–9 μ, brown, pale brown to olive-brown, terminal cells hyaline, subhyaline to yellowish, ends rounded, basal cell frequently provided with a short remnant of the separating cell, apical cell with top somewhat thickened and dark (see FIG. 1, C and E), at times bearing 1–3 hyaline, lateral, erect or divergent setae or appendages which vary in length from 20–760 μ or more and are about 1.5–2.5 μ in diam.

Specimen examined: *Harkness 2349* (TYPE), on decaying bark of *Eucalyptus globulus*, San Francisco, Calif., Dec. 1883, from the Ellis Collection, New York Botanical Garden.

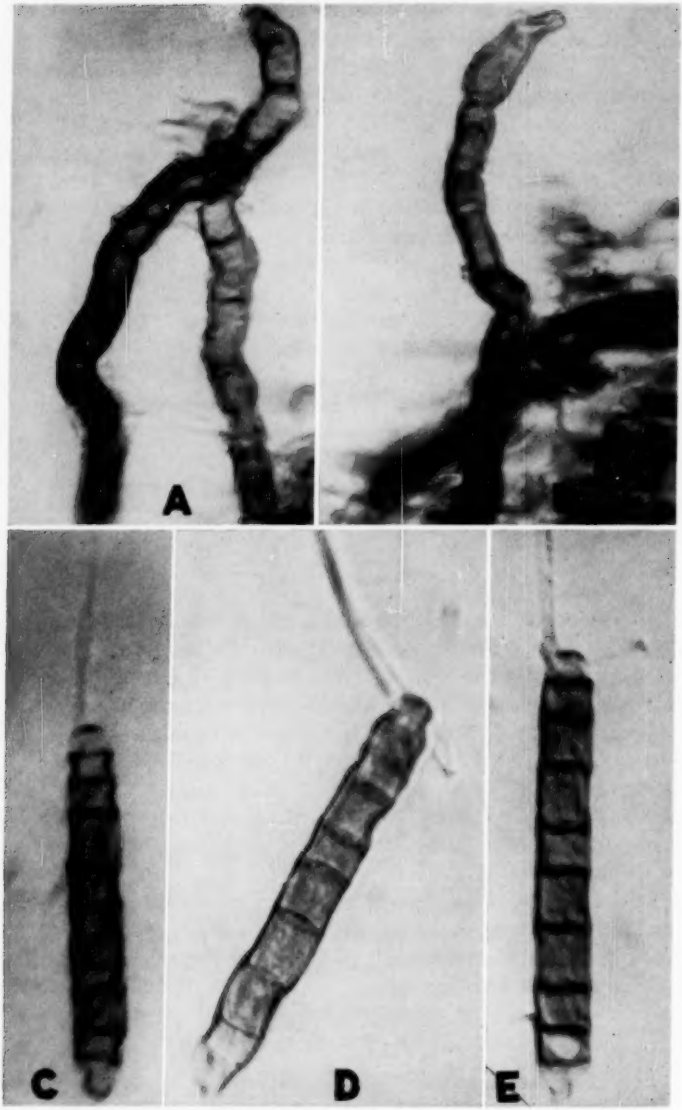


FIG. 1. *Composporium antennatum* Harkn. Photomicrographs of type. A and B. Conidiophores. C—E. Conidia. ×645.

The "spiral pedicels" or separating cells described by Harkness as attaching the conidia to the conidiophores have not been seen. The remnants of these cells are, however, as pointed out by Hughes (**9**), present on many of the conidia. Hughes in his study of the type describes them as "somewhat coiled."

Neither Harkness nor Hughes mentioned the extreme length of some of the conidial appendages. They are very delicate in appearance and are probably frequently broken off in the preparation of slides. The real nature of these setae or appendages is not apparent. They have no resemblance to germ tubes. Neither do they appear to be of the same nature as the septate appendages described and figured by Hughes for the three additional species included in the genus by him.

Based on the study of the type species and on the study by Hughes, a more complete diagnosis of the genus than that given by Harkness follows:

CAMPOSPORIUM Harkn.

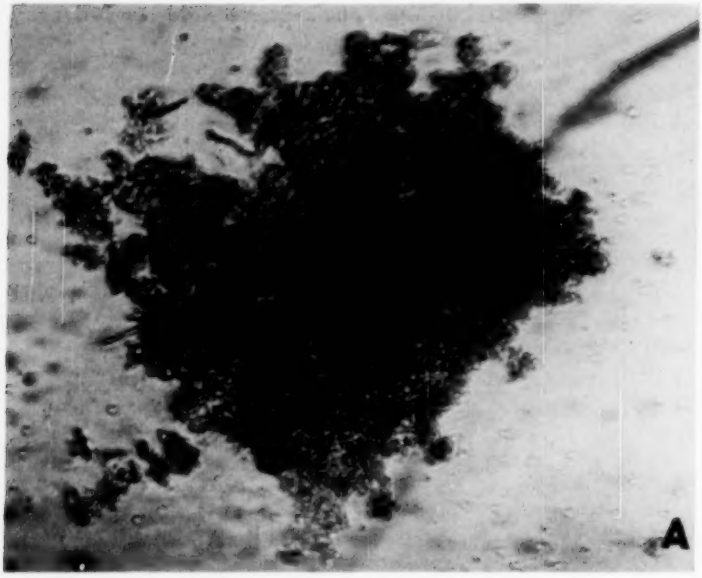
Conidiophores simple to sympodial, somewhat aggregated or diffuse on the vegetative hyphae and arising at right angles to them, [or "as hyphae which turn up away from the substratum and function as conidiophores" (Hughes **9**)], apexes attenuated or abruptly tapering to produce a short, narrow, straight or somewhat coiled disjointor or separating cell; conidia cylindrical, subcylindrical to cylindric-fusiform, several-septate, hyaline to brown, with basal and apical cells hyaline or lighter colored than the other cells, apical cell with or without erect to divergent lateral setae or appendages.

Hughes (**9**, p. 16) points out that *Camposporium* Harkn. may be the same as *Hymenopodium* Corda, the type of which is *H. sarcopodioides* Corda. The problem can only be resolved by an examination of the type of the latter.

Unfortunately Clements and Shear (**6**, pp. 216, 396) changed the spelling of *Camposporium* Harkn. to *Camarosporium* Harkn. even though the latter name had been used by Schulzer for a genus of the Sphaerioidaceae. Ainsworth and Bisby (**1**) list both *Camarosporium* Harkn. and *Camarosporium* Schulz. as well as *Camposporium* Harkn. In the latest edition of their book (**2**), *Camarosporium* Harkn. has been deleted.

TROPOSPORIUM

Troposporium Harkn., Bull. Calif. Acad. Sci. **1**: 39. 1884; Kellerman, Jour. Mycol. **1**: 30. 1885; Saccardo, Syll. Fung. **4**: 729. 1886;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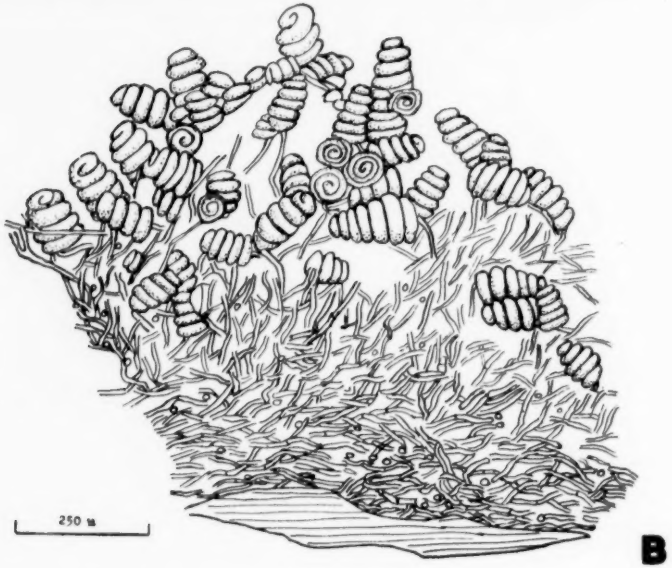
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Morgan, Jour. Cinc. Soc. Nat. Hist. **15**: 52. 1892; Lindau, in Engler and Prantl, Nat. Pflanzenfam. **1:1****: 510. 1900; Linder, Ann. Mo. Bot. Gard. **16**: 345. 1929; Moore, Mycologia **47**: 93. 1955.

The type species is *Troposporium album* Harkn., Bull. Calif. Acad. Sci. **1**: 39. 1884; Kellerman, Jour. Mycol. **1**: 30. 1885; Saccardo, Syll. Fung. **4**: 729. 1886; Morgan, Jour. Cinc. Soc. Nat. Hist. **15**: 52. 1892. *Fig. 21;* Linder, Ann. Mo. Bot. Gard. **16**: 345. 1929. *Fig. 17;* Moore, Mycologia **47**: 93. 1955.

The following description of the genus and species was given by Harkness:

"Sporodochium flattened, farinaceous. Hypha elongated, lax, branching. Spores spiral, attached to the hypha by slender pedicel-like branchlets.

"Allied to *Fusisporium*, but with different spores.

"*Troposporium album.*

"Acervuli white, 1–2 mm., often confluent, thick, branching freely, without septa, containing numerous granules and oil globules which are set free by breaking; spore—a long tube, granular, nucleolate without septa, μ 7 wide, coiled in a long spiral of 3–7 turns, flattened at the crossings, forming an oblong mass, with crenate borders. μ 40–45 × 18–22.

"On dead stems of Corylus rostrata. Sausalito, Dec. Feb. . . . 2929."

Based on a study of the type species the genus is redescribed as follows:

TROPOSPORIUM Harkn.

Sporodochia superficial, verruciform to pulvinate, gelatinous when fresh, horny when dry; hyphae flexuous, branched, septate; conidiophores arising as short branches of the hyphae and scarcely differentiated from them; conidia borne at the tips of the conidiophores, consisting of a long nonseptate tube coiled in three planes to form a compact, oblong, ellipsoidal to somewhat conical spore body.

The genus is intermediate between *Helicoon* and *Hobsonia*. The fruiting body is of the same type found in *Hobsonia* and the conidia are coiled as in *Helicoon*. It differs from both in that the conidia are nonseptate. This character by itself is hardly enough to warrant generic

FIG. 2. *Troposporium album* Harkn. A. Sporodochium, photomicrograph of smear preparation of type. B. Sporodochium, camera-lucida drawing of a section of specimen in Ellis Collection, New York Botanical Garden.

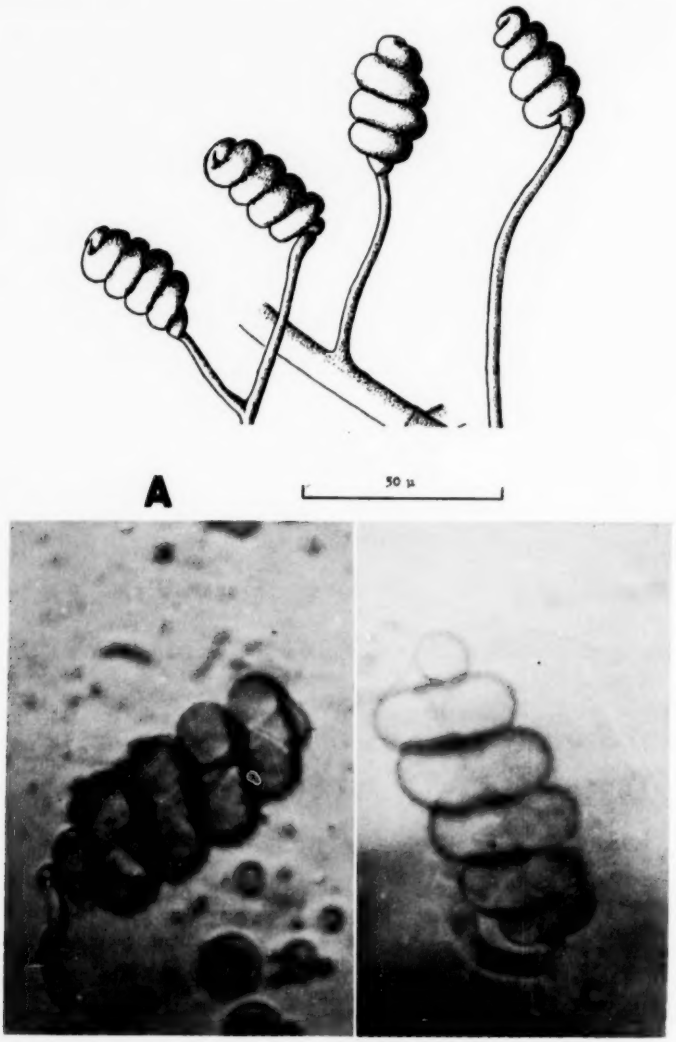

FIG. 3. *Troposporium album* Harkn. A. Conidiophores and conidia, camera-lucida drawing of type. B and C. Conidia and parts of conidiophores, photomicrographs of type, × 645.

status but the combination of characters given probably is sufficient to justify the genus.

TROPOSPORIUM ALBUM Harkn. FIGS. 2 and 3.

Sporodochia superficial, verruciform to pulvinate, 0.25–2 mm in diam., coalescing, gelatinous when moist, horny when dry, surface farinaceous, at first whitish, becoming cinnamon-brown with age, the radiating margins somewhat lighter in color, in appearance like a young stage of a brown thelephoraceous fungus; the sporodochia (FIG. 2, A and B) in section consisting of a lower $\frac{1}{3}$–$\frac{1}{2}$ of fairly compactly interwoven hyphae in which the hyphae in the lower portion run parallel to each other and to the substrate and turn upward in the upper portion, and the upper $\frac{1}{2}$–$\frac{2}{3}$ a conidial mass, the whole permeated by a gelatinous secretion which is brownish in age and produces a tough, compact mass with the free ends of some of the uppermost conidia giving a farinaceous aspect; hyphae hyaline to dilute brownish; conidiophores slightly flexuous, occasionally branched, continuous, arising as narrow branches of the hyphae, about 3–4 μ in diam., hyaline to dilute brownish; conidia consisting of a long, continuous tube, hyaline to dilute cinnamon brown, 7–9 μ in diam., coiled (3–)4–6(–7) times to form an oblong or ellipsoidal, or less frequently a conical spore body, 36–45 × 16–22 μ, with crenate or undulate margins.

Specimens examined: *Harkness 2929* (TYPE), on dead stems of *Corylus rostrata*, Sausalito, Calif., Dec. Feb. 1881, Calif. Acad. Sci. No. 2469; Harkness, on dead *Corylus* wood and bark, Sausalito, Calif., Dec. & Feb., Ellis Collection, New York Botanical Garden.

Linder (**14**, p. 345) in his "Monograph of the Helicosporous Fungi Imperfecti" accepts the genus and species, based on Morgan's (**15**) earlier study. He states that "there is only one species, the type of which has been lost." As pointed out earlier, the latter part of his statement is obviously incorrect as the type has been preserved at the California Academy of Sciences and what appears to be a part of the type collection is also in the Ellis Collection at the New York Botanical Garden.

THECLOSPORA

*Thecl*ospora Harkn., Bull. Calif. Acad. Sci. **1**: 41. 1884; Kellerman, Jour. Mycol. **1**: 30. 1885; Saccardo, Syll. Fung. **4**: 679. 1886; Lindau, in Engler and Prantl, Nat. Pflanzenfam. **1:1****: 503. 1900.

Harkness described the genus as follows:

"Spores surrounded by a cleft, hyaline border, borne on slender branching hyphae, compacted into a globular woolly mass."

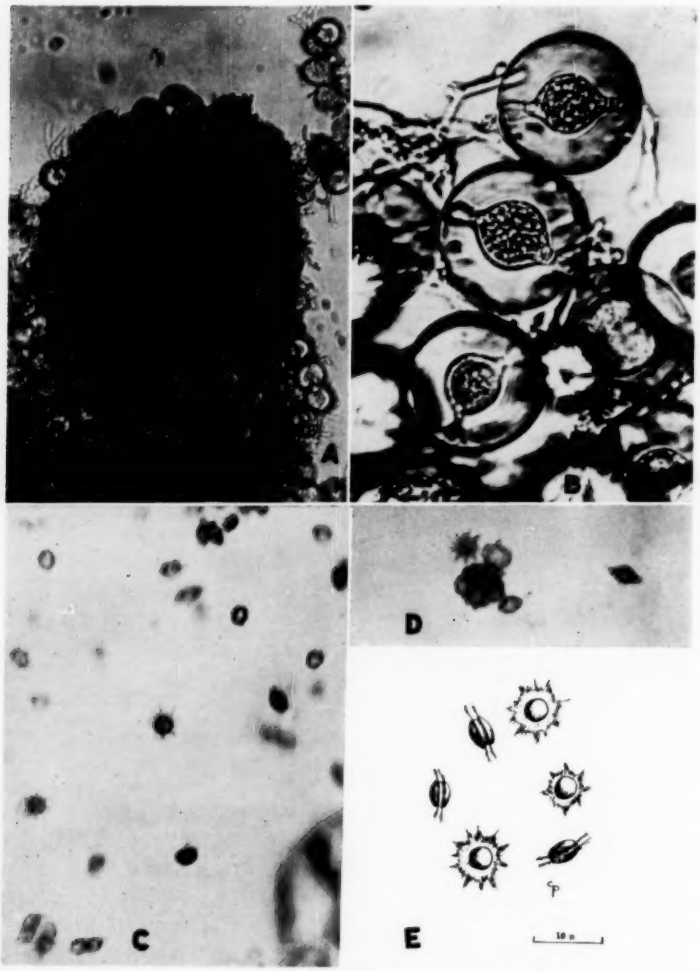

FIG. 4. *Theclospora bifida* Harkn. A–D. Photomicrographs of type. A. Cleistothecium and hülle cells. B. Hülle cells. C. Ascospores. D. Ascus and ascospores. E. Ascospores, camera-lucida drawing from type.

The type species is *Theclospora bifida* Harkn., Bull. Calif. Acad. Sci. **1**: 41. 1884; Kellerman, Jour. Mycol. **1**: 30. 1885; Saccardo, Syll. Fung. **4**: 679. 1886.

An examination of the type specimen reveals the "spores" described by Harkness to be the hülle cells of an *Aspergillus, Emericella* or *Eurotium*. The specimen contains no conidial stage but does have mature cleistothecia, asci, and ascospores. A description of the type follows:

THECLOSPORA BIFIDA Harkn. FIG. 4.

Fungal heaps superficial, scattered, globose, 0.25–2 mm in diam., brownish-yellow, composed of hülle cells and entwined hyphae and occasionally containing cleistothecia; cleistothecia brown to dark brown but when mature frequently appearing purplish-black from the contained ascospores, thin-walled, brittle, 200–435 μ in diam., breaking readily to release masses of ascospores and occasionally an ascus; ascospores purple, lenticular, 3.75–4.75 × 2.75–3.5 μ, encircled by two equatorial crests 2.5–3.5 μ in width, fimbriate-stellate in appearance; hülle cells circular to rarely oval in outline, thick-walled, hyaline, 20–40 μ in diam., walls 6–16 μ thick, the lumens 6–18 μ in diam.

Specimens examined: *Harkness 3612* (TYPE), on decaying leaves of *Eucalyptus globulus*, Golden Gate Park, San Francisco, Calif., Jan. 1883, Calif. Acad. Sci. No. 3159 and *Harkness 3612a*, on rotting leaves of *Eucalyptus globulus*, San Francisco, Calif., Dec. 1883, Calif. Acad. Sci. No. 7128.

Both of the above specimens were originally designated as No. 3612. The "a" after the number of the second specimen was added by the junior author in order to distinguish it from the type. The original description cites "San Francisco, Dec. . . . 3612." This would indicate that the second number should be the type. However, the packet designated as No. 3612 above was marked "type" and the other, No. 3612a as "part of type." Furthermore, No. 3612 contains mature cleistothecia and ascospores whereas No. 3612a consist mainly of sterile masses of hülle cells, and rarely, very young cleistothecia.

The description given above agrees well with the description given by Thom and Raper (**16**, p. 163) for *Aspergillus variecolor* (Berk. et Br.) Thom et Raper. It differs from their description in the character of the wall of the cleistothecium, which they describe as: "when stripped of enveloping cells purple-red, brittle, *composed of a single layer of cells*" (the italics are ours). The wall of the cleistothecia of the Harkness material is composed of several layers of compacted cells as described for this species by Benjamin (**3**, pp. 671, 679). This character is a part of the combination of characters given by Benjamin in validating the ascomycetous genus *Emericella* Berk. et Br.

The ascospores of the Harkness material agree in size of spore body and equatorial crests with the dimensions given by Thom and Raper but have a fimbriated margin (see FIG. 4, E) not mentioned by these authors. This difference may have varietal significance but is, for the present at least, interpreted as being within the varietal limits of the species.

The absence of a conidial apparatus is well within the limits of variability of the species set by Thom and Raper. The conclusion reached by the authors is that *Theclospora bifida* Harkn. is a synonym of *Emericella variecolor* Berk. et Br., or of *Aspergillus variecolor* (Berk. et Br.) Thom et Raper, and that the genus *Theclospora* Harkn. is a synonym of *Emericella* Berk. et Br.

The spelling of *Theclospora* was changed by Saccardo (Syll. Fung. **4**: 679) to *"Thecopsora."* Clements and Shear (**6**, p. 406) use the spelling *"Thelospora."*

Theclospora lateralis Harkn., Bull. Calif. Acad. Sci. **1**: 163. 1885; Saccardo, Syll. Fung. **4**: 679. 1886.

The second species of the genus was published by Harkness in 1885. A redescription of this species based on a study of its type follows:

THECLOSPORA LATERALIS Harkn. FIG. 5.

Fungal heaps sphaerical, whitish-brown, 0.25–1 mm in diam., consisting of masses of hülle cells, hyphae, conidiophores and conidia; conidial heads hemisphaerical, 30–60 μ wide; conidiophores straight to somewhat sinuous, smooth-walled, hyaline, 4.5–6 μ in diam. below, 7–9 μ in diam. just below the vesicle, 105–222 μ long; vesicles obovate to hemisphaerical, 12–15 × 18–21 μ, sterigmata in two series; conidia greenish, globose, 3–4.5 μ in diam., smooth-walled; hülle cells very abundant, irregularly circular to ovoid in outline, 18–30 × 14–27 μ, walls 4–12 μ thick, lumens 6–15 μ in diam., with a single, lateral cleft at the attachment of the hypha.

Specimen examined: *Harkness 3632* (TYPE), on rotting stems of *Nerium oleander*, Oakland, Calif., Feb. 1883, Calif. Acad. Sci. No. 3177.

Apparently, Harkness interpreted the presence of the *Aspergillus* as being secondary and based the species on the hülle cells. No cleistothecia were present in the material. If one assumes that they are not produced, then the characters of the conidia, conidiophores and hülle cells are the main criteria to use in placing the species. On the basis of the available characters, as set forth in the description above, the

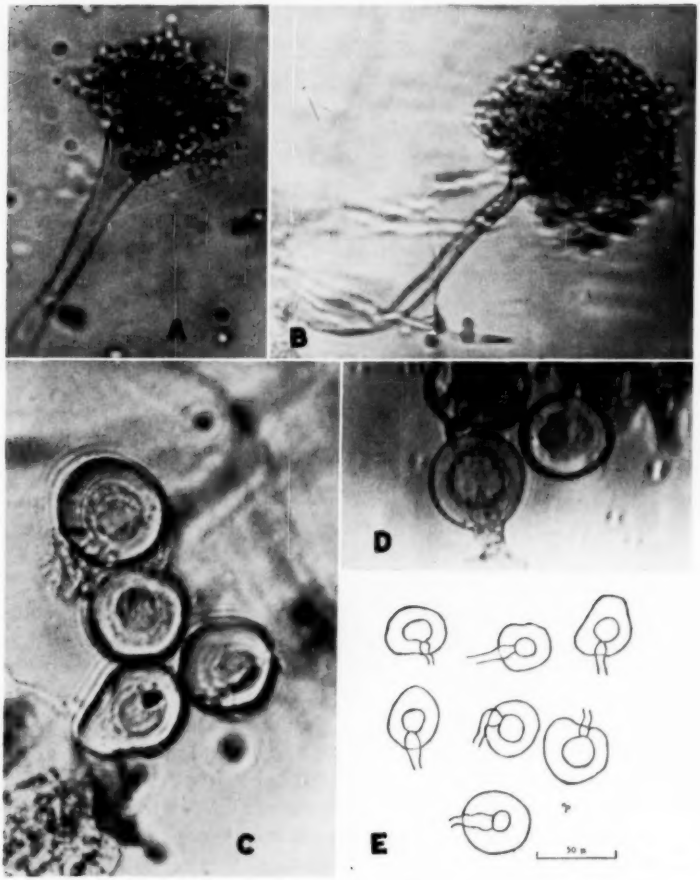

FIG. 5. *Thecospora lateralis* Harkn. A–D. Photomicrographs of type. A and B. Conidiophores and conidial heads. C and D. Hülle cells. E. Hülle cells, camera-lucida drawing.

fungus belongs in the *Aspergillus versicolor* group of the Thom and Raper Manual (**16**, pp. 183–194). In this group it best fits *A. versicolor* (Vuill.) Tiraboschi and could be this species. In any event the combination **Aspergillus lateralis** (Harkn.) Peek et Solh. comb. nov. becomes necessary.

CLEISTOSOMA

Cleistosoma Harkn., Bull. Calif. Acad. Sci. **1**: 41. 1884; Kellerman, Jour. Mycol. **1**: 30. 1885; Saccardo, Syll. Fung. **9**: 943. 1891.

The type species is *Cleistosoma purpureum* Harkn., Bull. Calif. Acad. Sci. **1**: 41. 1884; Kellerman, Jour. Mycol. **1**: 30. 1885; Saccardo, Syll. Fung. **9**: 943. 1891.

Harkness describes the genus and species as follows:

"Perithecia orbicular, membranaceous. Asci borne on branching threads, globose, evanescent. Sporidia hemisphaerical, echinulate.

"*Cleistosoma purpureum.*

"Perithecia purple black, very delicate, soon dehiscent, developed within the heaps of Cleistosoma purpureum, which it stains purple; asci globular, hyaline, 8-spored, μ 9–12: sporidia purple, hemisphaerical, long-echinulate round the disk margin. μ 3–4. 3606.

"The relation of this fungus to the preceding is still in doubt. I suspect it may be the same as that of Eurotium to Aspergillus."

The preceding fungus referred to is *Theclospora bifida* Harkn. After describing it Harkness states: "The place of this fungus is very uncertain, and it is only placed here because of its connection with the next."

The TYPE material of *Cleistosoma purpureum* consists of two packets, both numbered 3606. As a matter of convenience these have been designated as follows: *3606. Cleistosoma purpureum* Harkn., on rotting leaves of *Eucalyptus*, San Francisco, Calif., Dec. 1882; Calif. Acad. Sci. No. 7297: and *3606a. Cleistosoma purpureum* Harkn., on rotting leaves of *Eucalyptus*, Golden Gate Park, San Francisco, Calif., Jan. 1884; Calif. Acad. Sci. No. 3154.

The specimen numbered 3606a has a few small golden heaps of the fungus present, consisting of hülle cells and a few very young cleistothecia. No asci nor ascospores were found. A drawing of an ascus and contained ascospores inside the packet indicates the authenticity of the specimen. The other packet contains mature cleistothecia. These can be seen with the naked eye, or at least with a hand lens, as dark spots near the tops and centers of the fungal heaps. The heaps are scattered, brownish-yellow or golden-brown, 0.25–1.5 mm in diam. The cleistothecia are sphaerical, brownish but appearing purple-black from the contained ascospores, 250–357 μ in diam.; asci globose to elliptical, 9–13 × 8.2–12 μ; ascospores lenticular, 3.3–4 × 2.2–3 μ, with two equatorial, stellate crests, 1.7–3 μ wide; hülle cells circular to subcircular in outline, marked with concentric striae, cleft on opposite sides or at various angles, apparently being intercalary in origin, 23–41 μ in diam., walls 4–13 μ thick, lumen 8–20 μ in diam.

The specimen described above is apparently fairly young as the asci are intact and not yet evanescent. It agrees well with the specimen of *Theclospora bifida* Harkn. with which Dr. Harkness associated it as the possible ascigerous stage. The crests of the ascospores are not fimbriate-stellate as in *T. bifida* but this could be merely a factor of age as the specimen of the type of *T. bifida* is quite mature as evidenced by the evanescent asci. The two appear to be the same and *Cleistosoma purpureum* Harkn. is, therefore, placed in synonomy with *Emericella variecolor* Berk. et Br. as was *T. bifida* Harkn. The genus *Cleistosoma* Harkn. is a synonym of *Emericella* Berk. et Br.

DICRANIDION

Dicranidion Harkn., Bull. Calif. Acad. Sci. **1**: 163. 1885; Kellerman, Jour. Mycol. **1**: 71. 1885; Saccardo, Syll. Fung. **4**: 728. 1886; Lindau, in Engler and Prantl, Nat. Pflanzenfam. **1:1****: 510. 1900; Hughes, Can. Jour. Bot. **31**: 607. 1953.

The type species is *Dicranidion fragile* Harkn., Bull. Calif. Acad. Sci. **1**: 163. 1885; Kellerman, Jour. Mycol. **1**: 71. 1885; Saccardo, Syll. Fung. **4**: 728. 1886; Hughes, Can. Jour. Bot. **31**: 607. 1953. *Fig. 36.*

Harkness describes the genus and species as follows:

"(*Etym. Dikranos,* a fork).

"Acervuli pale, scattered. Spores hyaline, septate, shaped like a tuning-fork, attached by the closed extremity to a short branching hypha.

"*Dicranidion fragile.*

"Acervuli, rosey-white, minute, scattered; spores hyaline, 4-septate, shaped like a tuning-fork, attached by the closed extremity, easily separating, each arm dividing near the center and near the base, forming one rounded and four oblong segments; length of spore 12–16: width of arm, 4–5 μ.—On decaying *Nerium Oleander,* Oakland, Feb. 3631.

"In appearance much like *Fusarium.*"

Based on a study of the type specimen and on a study made by the late Dr. S. C. Damon (communication to the junior author), the genus is emended as follows:

DICRANIDION Harkn. emend.

Mycelium superficial or innate, sparse to abundant; hyphae branched, septate, hyaline or light-colored, effuse or aggregated into sporodochium-like units: conidiophores single or clustered, erect or ascending, short or long, smooth or denticulate in upper portion, hyaline or light-colored, septate, monopodial or sympodial or both: conidia borne terminally or by

sympodial development of the conidiophore becoming laterally displaced, several- to many-celled, mostly 2–3-lobed, in some species multi-lobed, lobes parallel, arising from a common biconic or elongated basal cell, basal cell and lobes septate or nonseptate, hyaline or light-colored.

According to Damon the genus *Pedilospora* Höhn. (**11**, p. 1047) is a synonym of *Dicranidion* Harkn. This has also been indicated by Hughes (**10**, p. 607).

The above description has been drawn to include the enlarged scope of the genus presented by the addition of the species recognized by Damon.

The genus should be placed in the *Moniliaceae* rather than in the *Tuberculariaceae* where Saccardo placed it.

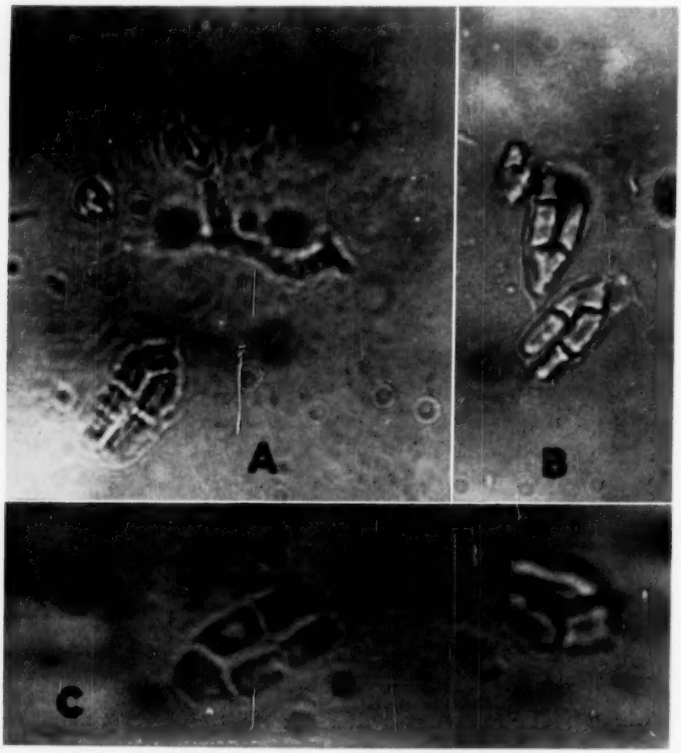

FIG. 6. *Dicranidion fragile* Harkn. Photomicrographs of type. A. Conidiophore and conidia. B and C. Conidia. A and B, × 980; C, × 1470.

DICRANIDION FRAGILE Harkn. FIGS. 6–7.

Syn. *Pedilospora ramularioides* Bubák, Ann. Myc. **14**: 156. 1916. *Abb. 2, figs. 1–3;* Saccardo, Syll. Fung. **25**: 750. 1931.

Sterile hyphae sparse to fairly abundant, branched, septate, repent, effused or forming minute, pulvinate tufts with strands of hyphae radiating from their bases and at times connecting with adjacent tufts, giving an arachnoid appearance, rosy-white to yellowish-white; conidiophores erect to ascending, sympodial with the terminal branches forming lateral denticulae, occasionally with monopodial branching, solitary or conglutinated into irregular fascicles, septate, geniculate in upper denticulate region, hyaline, 12–25 × 1.5–3 μ; conidia hyaline, ovate to ellipsoid in overall appearance, 9–18 × 6–8 μ, consisting of a nonseptate basal cell to which are attached two or rarely three, erect, parallel lobes; lobes incurved at the distal ends, rarely touching, continuous or 1(–2)-septate.

On rotting wood, often along with other fungi or growing upon them.

Specimen examined: *Harkness 3631* (TYPE), on *Nerium oleander* L., Oakland, Alameda County, Calif., Feb. 1882, Calif. Acad. Sci. No. 3176.

The authors have not seen a specimen of *Pedilospora ramularioides* Bub. The description given by Bubák (**4**) is, however, very complete

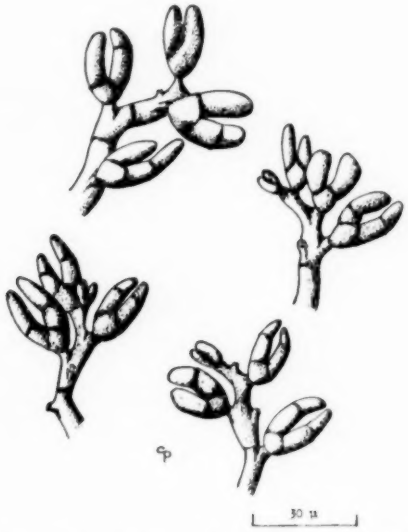

FIG. 7. *Dicranidion fragile* Harkn. Conidiophores and conidia, camera-lucida drawings of type.

and the fungus well illustrated. There appears to be no question as to its identity with the Harkness fungus. Bubák states that it is a parasite on *Bispora pusilla* Sacc. on old wood of *Castanea vesca*. It is interesting to note that the Harkness specimen has several species of associated fungi, one of which is a species of *Bispora*.

It is quite possible that the type species of the genus *Pedilospora*, *P. parasitans* Höhn., as well as *P. episphaeria* Höhn. (**12**, p. 358; **13**, p. 26), are also synonyms of *Dicranidion fragile* Harkn. Von Höhnel in describing *P. episphaeria* states: "Die drei bisher bekannten *Pedilospora*-Arten, *P. parasitans* Höhn., *P. ramularioides* Bub. und die eben beschriebenen wachsen alle auf Pilzen und sind auch mit der Lupe nicht zu sehen. Ob sie spezifisch voneinander verschieden sind oder nur Formen einer Art darstellen, müssen weitere Funde derselben entscheiden."

The spelling of *Dicranidion* was changed to *Dicranidium* by Clements (**5**, p. 161).

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A METHOD OF OBTAINING PURE RADIOACTIVE β-CAROTENE USING PHYCOMYCES BLAKESLEEANUS [1, 2]

VIRGIL GREENE LILLY, H. L. BARNETT, R. F. KRAUSE, AND F. J. LOTSPEICH

(WITH 2 FIGURES)

Many species of fungi synthesize carotenoids (Goodwin, **1952, 1954**). The role of these compounds in the fungi which synthesize them is obscure. Carotenoid pigments are frequently found in, or associated with, spores and fruiting structures as well as in the mycelium. Apparently, animals do not synthesize carotenoid pigments and are dependent upon an exogenous source of β-carotene and a few other carotenoids as precursors of vitamin A. The role of vitamin A in vision (rhodopsin) is the best established metabolic function of this compound. Recently, Wolf *et al.* (**1957**) have concluded that vitamin A is involved, directly or indirectly, in the reversal of glycolysis between the triose and glucose stages. It is suspected that vitamin A, and perhaps β-carotene, play other essential roles in many metabolic processes in animals. Support for this belief stems in part from investigations dealing with the distribution and metabolism of radioactive β-carotene in the chicken (Laughland, **1954**) and in the rat (Krause and Sanders, **1957**; Laughland and Wilmer, **1957**). These authors found C^{14} from labeled β-carotene to be incorporated into such compounds as fatty acids, sterols, carbon dioxide, and unidentified water-soluble compounds. The use of radioactive β-carotene is essential for the continuation of these and other metabolic studies of β-carotene and vitamin A.

At present, radioactive β-carotene is apparently unavailable from commercial sources. In view of the need for a simple and reliable method of producing adequate amounts of this material for animal investigations, it was thought that the use of a suitable fungus for the biosynthesis of radioactive β-carotene would be advantageous with re-

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spect to time and equipment and the ease with which nutritional and environmental factors may be controlled.

Apparently, the only species of fungi that have been used to produce radioactive β-carotene are *Mucor hiemalis* (Grob and Bütler, **1954**, **1954a**) and *Phycomyces blakesleeanus* (Grob *et al.* **1951**; Glover *et al.* **1951**; Chichester *et al.* **1956**). The origin of the various carbon atoms in the β-carotene molecule is being actively investigated by the use of various C^{14}-labeled precursors (Grob *et al.* **1952**; Grob and Bütler, **1955**, **1956**; Yokayama *et al.* **1957**; and Wuhrmann *et al.* **1957**). For theories concerning the pathways of biosynthesis of β-carotene from acetate, see Grŏb (**1956**).

The purpose of this paper is to describe a method for the production of pure C^{14}-labeled β-carotene suitable for chemical and certain types of biological investigations.

MATERIALS AND METHODS

Cultural conditions: An isolate of *Phycomyces blakesleeanus* Burgeff (No. 104, West Virginia University stock culture collection) was used in all of this work. Spore suspensions in water were used as inoculum. The spores were collected from 2- to 3-week-old cultures grown on malt-extract-yeast-extract-agar medium. The spore suspensions were stored in screw-capped test tubes and kept in the freezing compartment of a refrigerator; such spore suspensions may be used for 12 months or longer without great reduction in germination.

The basal medium used had the following composition: D-glucose, 10 g; potassium acetate, 0.72 g; $(NH_4)_2SO_4$, 1 g; KH_2PO_4, 1 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; Fe^{+++} and Zn^{++}, 0.1 mg each; Mn^{++}, 0.05 mg; Ca^{++}, 10 mg; thiamine, 100 μg; and double distilled water, q.s. 1000 ml. The pH of the medium was adjusted to 5.7 to 5.8 before autoclaving. The pH value of the medium was between 5.5 and 5.6 after autoclaving.

The basal medium was machine pipetted into acid-washed 250-ml Erlenmeyer flasks; each flask received 25 ml of medium. The flasks were capped with 50-ml beakers. The medium was autoclaved for 15 minutes at 121° C. Each flask was inoculated with one drop of spore suspension. The inoculated flasks were stored in tote boxes, each of which held 20 flasks, and incubated in a stainless-steel hood in the isotope laboratory of the Physics Department. The cultures were illuminated 24 hours daily by two 40-W white fluorescent lamps (50 to 70 f.c.), and the temperature was maintained at 25 ± 1° C.

Some variation in the initial rate of growth and carotenogenesis was found among the different experiments. For this reason, a sufficient

number of control cultures were included in each experiment so that daily determinations could be made of dry weight of mycelium, pH of the culture filtrate, residual glucose, and carotene content of the mycelium. In some experiments the nitrogen content of the culture medium and the lipid content of the mycelium were determined. Growth was measured by weighing the mycelium from duplicate flasks after drying at 100° for 24 hours. The pH of the culture medium was determined with a Cambridge pH meter. Residual glucose in the medium was determined by the method of Folin-Wu (Keller, **1951**). Residual nitrogen in the medium was determined by a micro-Kjeldahl procedure. The lipid content was considered to be the difference in weight of dry mycelium before and after exhaustive extraction with diethyl ether in a Soxhlet extractor.

The method of Garton *et al.* (**1951**) was used for the daily determination of the carotene content of the mycelium. The mycelium was ground in a mortar with peroxide-free diethyl ether until it was colorless. The ether extracts were kept in glass-stoppered graduates of Low-actinic Pyrex glass until measured. The carotene content of the mycelium was calculated from the optical density of the extracts, measured at 452 mμ with a Beckman model DU spectrophotometer which had been calibrated with a sample of pure β-carotene.

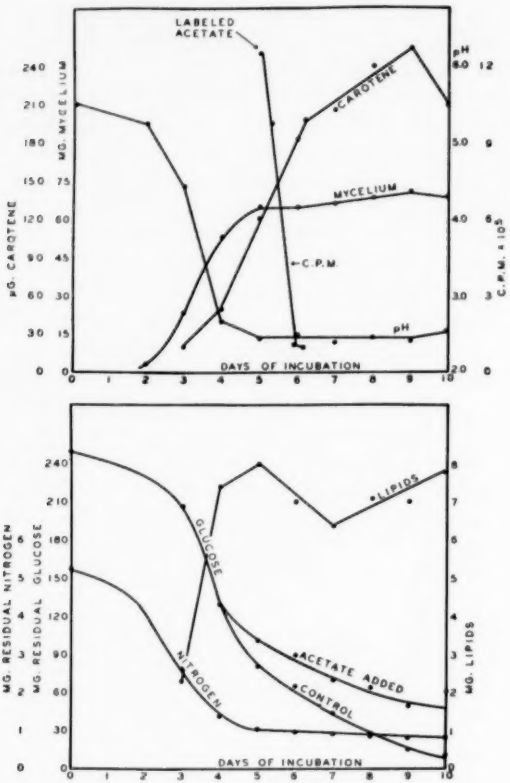
A solution of potassium acetate was prepared which contained 12.2 mg/ml. Before autoclaving, the potassium-acetate solution was acidified with hydrochloric acid until the pH was 2.7 to 2.8. This treatment converted most of the potassium acetate into potassium chloride and acetic acid. One ml of acidified potassium acetate was added daily to each flask when the dry weight of the mycelium reached 50 to 60 mg. This usually occurred on the fourth day of incubation. Care was taken to flow the solution down the sides of the flasks. After the addition of the acidified potassium acetate solution one end of the box that contained 20 flasks was slowly raised 4 inches from horizontal, and then slowly lowered. This procedure mixed the acidified potassium acetate with the medium; this operation must be done carefully to avoid disturbing the mats of mycelium.

Labeled sodium acetate (specific activity about 5 mc/m mole) was made up in a solution of the desired radioactivity, autoclaved, and one ml aliquots dispensed to each culture by means of a Cornwall syringe. Care was taken to flow the solution of labeled acetate down the sides of the flasks. The labeled acetate was added on the fifth day immediately after the addition of acidified potassium acetate. The tote boxes were not tilted until both additions of acetate had been made.

The concentration of labeled acetate remaining in the culture medium was determined at intervals. Labeled and carrier acetate were probably utilized at the same rate. Samples (0.5 ml) of medium containing labeled acetate were obtained with sterile pipettes. Aliquots (0.1 ml) were transferred to planchettes, neutralized (phenolphthalein) with sodium hydroxide, and dried under an infrared lamp. The samples were counted with a Tracerlab windowless gas-flow counter. The radioactivity is reported as counts per minute (C.P.M.) per flask corrected for background (FIG. 1). The radioactivity of samples of carotene was measured with the same instruments.

Isolation of β-carotene: Twenty-eight hours after the addition of labeled acetate the mycelium was collected on a fluted filter, pressed damp-dry, and placed in methanol. The radioactive β-carotene was extracted and purified in the following manner: The mycelium was dehydrated thoroughly with methanol and exhaustively extracted with redistilled petroleum ether (b.p. 35 to 37° C). The extract was concentrated to 30 ml in a Rinco evaporator under reduced pressure and then saponified by refluxing under dim red light with 2 *N* potassium hydroxide in ethanol for 90 minutes. The saponification mixture was cooled, and diluted with an equal volume of water and the unsaponified materials were extracted with petroleum ether. The petroleum-ether extract was washed with aqueous 0.5 *N* potassium hydroxide and then with distilled water until the washings were neutral to phenolphthalein. The extract was dried with anhydrous sodium sulfate, treated with tricalcium phosphate (Mitchell *et al.* **1953**) and then passed through a column of bone meal (Glover *et al.* **1948**). The extract was then evaporated to dryness under vacuum; the residue was washed 5 times with 5 to 10 ml portions of cold methanol containing one per cent of petroleum ether. The methanol-insoluble material was redissolved in petroleum ether and concentrated under vacuum to about 30 ml, at which time β-carotene started to crystallize. Crystallization was allowed to continue in the dark at −20° C for several days. The β-carotene crystals were collected on a sintered glass filter and washed 5 times with 5 to 10 ml portions of cold methanol. The crystals were redissolved in petroleum ether and the solution made to a known volume. The (1%, 1 cm) value,[3] and the radioactivity of suitable aliquots were

[3] Booth (**1957**) defines the E (1%, 1 cm) value as "the hypothetical extinction or optical density of a 1% (weight in volume) solution of the carotenoid with a 1 cm optical path at the wavelength (usually) of maximum extinction." It is a useful criterion of purity.



FIGS. 1–2. The data are average values from two or more cultures. FIG. 1 (above) presents data for the production of mycelium, the accumulation of carotene, and the pH values of the culture medium during 10 days of incubation. Data are given for the utilization of acetate for the 28 hour period during which radioactive β-carotene was synthesized. FIG. 2 (below) presents the data for the residual amounts of glucose and nitrogen in the culture medium, and the accumulation of lipids in the mycelium as functions of the time of incubation. Note the sparing effect of added acetate on glucose utilization.

determined. The petroleum ether solution of the β-carotene was evaporated to dryness under nitrogen and stored under nitrogen at −20° in the dark.

EXPERIMENTAL RESULTS

The procedure described above is based on more than a dozen experiments in which radioactive β-carotene was prepared. These experiments were preceded by an extensive study of carotenogenesis by this isolate of *Phycomyces blakesleeanus*. Rather than attempt to summarize all of the available data one representative experiment will be described in some detail.

In this experiment 140 flasks were used. Seventy-eight flasks were used for the biosynthesis of radioactive β-carotene. The addition of acidified potassium acetate was started on the fourth day, and on the fifth day a total of 120 μc of labeled acetate (60 μc each of acetate-1-C^{14} and acetate-2-C^{14}) was added to the 78 cultures. The cultures were tilted after the addition of acetate as described in the previous section. The radioactive mycelium was harvested 28 hours after the addition of labeled acetate. The data for the separation and purification of radioactive β-carotene are summarized in TABLE I.

The E (1%, 1 cm) value of this sample of purified β-carotene was 2522. This value was calculated from the formula

$$\text{E (1\%, 1 cm)} = \frac{1}{\text{Conc. (1\%)} \times \text{length of cell in cm}} \times \text{optical density}$$

Various E (1%, 1 cm) values for β-carotene have been reported; Booth (**1957**) suggests that 2550 is a representative value. The spectrum of this sample of β-carotene in petroleum ether was obtained with a Beckman model DU spectrophotometer. The absorption curve corresponded closely with the curves for β-carotene given in the literature (Booth, **1957**).

TABLE I

THE PURIFICATION OF RADIOACTIVE β-CAROTENE. THE TOTAL RADIOACTIVITY ADDED TO THE MEDIUM WAS 104×10^6 C.P.M.

Step	Mg Carotene (Calculated from optical density)	C.P.M. (Total)
1. Petroleum-ether extract from mycelium	15.52	13,520,000
2. Petroleum-ether extract after saponification	14.00	1,825,000
3. Petroleum-ether extract after treating with calcium phosphate and bone meal	13.66	1,025,000
4. After washing with methanol containing 1% petroleum ether	7.92	587,500
5. Crystalline β-carotene	5.63	
	5.353 [1]	431,000

[1] Determined by weighing.

The remaining flasks were divided into 2 groups and were used as controls. Cultures in group I, starting on the fourth day, received daily 12.2 mg of acidified potassium acetate. Cultures in group II did not receive additional acetate. Both sets of controls were tilted daily. Harvests of the control cultures were continued until the tenth day. Inasmuch as the data from the two sets of controls were essentially the same only the data from the group I controls were used in FIG. 1 and 2. A single exception to the above statement deserves notice. Less glucose was utilized by the control cultures in group I which received the daily addition of acidified potassium acetate than by control cultures in group II. These data from both groups of controls are shown in FIG. 2.

FIG. 1 shows that the rapid production of mycelium decreased after the fourth day of incubation. By the fourth day, 75 percent of the mycelium had been produced. The pH of the medium decreased from 5.25 on the second day to 2.68 on the fourth day. By the fifth day the pH of the medium was 2.45 and thereafter it changed very slightly.

Only a little carotene was produced by the third day (20 μg/flask) but carotenogenesis was rapid between the third and sixth day. The maximum carotene content was reached on the ninth day (254 μg/flask). The corresponding yield for the control cultures in group II was 245 μg.

The added acetate was utilized rapidly (FIG. 1). On the assumption that the fungus did not distinguish between labeled and carrier acetate (isotope effect) the radioactivity of the medium is a measure of the amount of acetate utilized. Within 28 hours, at least 96 percent of the added acetate (carrier plus labeled acetate) was utilized. This value is probably too low inasmuch as any labeled metabolites including carbon dioxide liberated into the medium would be reported as acetate. Other experiments extending for 5 days showed that a trace of radioactivity remained in the medium. By adding labeled acetate to uninoculated medium (pH 2.5) it was found that little or no loss of radioactivity occurred within 5 days.

Glucose was utilized rapidly during the phase of rapid growth (FIG. 2). Half the glucose was utilized by the end of the fourth day. The utilization of glucose by the cultures in group I was slower than by control cultures in group II (FIG. 2). The control cultures in group II consumed 48 mg of glucose carbon between the fourth and tenth day. The control cultures in group I consumed about 30 mg of glucose carbon during the same time. In addition, the group I cultures utilized about 21 mg of acetate carbon during the same time. Thus, the amounts of carbon consumed by the two groups of controls were approximately

the same. This sparing effect of acetate on glucose has been confirmed repeatedly.

The utilization of nitrogen appeared to parallel glucose utilization until the sixth day, and thereafter there was but little change in the nitrogen content of the medium.

DISCUSSION

The amount of carotene synthesized by *Phycomyces blakesleeanus* is dependent upon the isolate used, the composition of the basal medium, the time of incubation, temperature, light, and other factors. Carotenogenesis follows the initial phase of rapid growth and continues after the phase of rapid growth (FIG. 1). Within limits, rapid growth and carotenogenesis appear to be separate processes. High yields of carotene have been obtained on the basal medium used, only when the rate and amount of growth were below maximum. By increasing the initial concentration of acetate in the basal medium to 0.02 *M* the production of mycelium was increased, normal asexual sporulation occurred, and the glucose in the medium was completely utilized within 5 to 6 days. The pH of the culture medium did not decrease as much under these conditions as when the basal medium was used. The addition of certain organic acids to media containing ammonium salts increases the yield of mycelium of *P. blakesleeanus* and other fungi (Leonian and Lilly, **1940**). The yield of carotene was low (<200 μg/flask) when the concentration of acetate was high enough to result in "normal" growth and sporulation. These results confirm those reported by Friend *et al.* (**1955**).

A low external pH (2.5 to 3.0) favors carotenogenesis and restricts growth of *P. blakesleeanus* but this is not true of all carotene-producing fungi. A low external pH decreases carotenogenesis by *Choanephora cucurbitarum*.

Only a few short sporangiophores are produced on the basal medium at 25°. Reducing the temperature of incubation to 20° increases asexual reproduction and reduces the yield of carotene by about 50 per cent. The weight of mycelium produced at 20 and 25° was about the same. High yields of carotene were obtained only when sporulation as well as growth was restricted. Conditions that limit growth and sporulation appear to divert the flow of nutrients from the pathways resulting in growth and sporulation, and channel them into the pathways leading to the formation of carotene and probably into other metabolic products.

The concentration of carotenoids in the mycelium is low even under the most favorable conditions for carotenogenesis. In these experi-

ments, the total carotene content of the mycelium did not exceed 0.3 to 0.35 percent. The conversion of any C^{14}-labeled carbon source into β-carotene may be expected to be low. No carbon sources are known which are converted exclusively into β-carotene. It is important, therefore, to use conditions that favor the incorporation of C^{14} from the labeled carbon source into β-carotene. Presumably, much of the precursor carbon is lost as carbon dioxide. A study of C^{14} loss as carbon dioxide may lead to a better choice of labeled carbon sources or time of addition of such source to the medium.

Since the amount of any precursor converted into β-carotene is small it is important to use a C^{14} source that is reasonable in cost, and that is an active precursor of β-carotene. Acetate meets these requirements reasonably well. Acetate will serve as the sole source of carbon for *P. blakesleeanus* (Schopfer and Grob, **1952**). The methyl and carboxyl carbons of acetate were used in equal amounts in the synthesis of β-carotene when *P. blakesleeanus* was cultured on a lactate-acetate medium (Grob *et al.* **1952**). Glover *et al.* (**1951**) found the methyl carbon of acetate to be in part transformed into β-carotene when mats of *P. blakesleeanus* were transferred to a glucose-acetate solution. These experiments have shown that both carbon atoms of acetate are converted, in part, into β-carotene by *P. blakesleeanus* in the presence of glucose.

Under the conditions used in this experiment, about one C^{14} atom out of 240 added as labeled acetate was recovered as pure β-carotene (TABLE I). The actual efficiency of *P. blakesleeanus* in incorporating C^{14} from labeled acetate into the β-carotene molecule was about 3 times as great as indicated above, since two-thirds of the β-carotene was lost in this experiment during purification.

The effect of the β-carotene present in the mycelium at the time of adding labeled acetate is to decrease the specific activity (C.P.M./mg) of the β-carotene isolated. From FIG. 1 it may be seen that the carotene content was 130 μg per flask when labeled acetate was added. Twenty-eight hours later at the time of harvest the carotene content was 198 μg per flask. Presumably, only the 68 μg of β-carotene synthesized during this 28-hour period was labeled. On this basis, the specific activity of the β-carotene isolated was about one-third as great as the β-carotene synthesized during the period of utilization of labeled acetate.

It is important to add labeled acetate after the growth phase is essentially complete. In other experiments in which labeled acetate was added at the time of inoculation the radioactivity of the β-carotene isolated was very low.

The efficiency with which labeled acetate was incorporated into the

β-carotene molecule varied as much as twofold among experiments. The reasons for this variation are not known. Presumably, this variation was due to differences in the relative activity of the pathways by which acetate is utilized. These pathways no doubt are manifold. While no quantitative studies were made, it was found that the residual mycelium after carotene extraction was radioactive. The fatty acids from the saponification step and the sterols from the bone meal column were found to be radioactive. A more intensive investigation of the fate of labeled acetate utilized by *P. blakesleeanus* should aid in determining the optimum conditions for the conversion of acetate into β-carotene.

The specific activity of the radioactive β-carotene produced by this method may be varied within wide limits. The radioactivity of the β-carotene, other conditions being equal, is directly proportional to the activity of the labeled acetate used. From 1 to 20 μc of labeled acetate per flask has been used in various experiments.

The amount of acetate that a 4- to 7-day-old culture is able to utilize in 24 hours imposes an upper limit on the amount of labeled acetate that can be added. A culture under the conditions used in this work utilized as much as 0.125 m mole of acetate in 24 hours. Using labeled acetate with a specific activity of 5 mc/m mole, it would be possible to use as much as 625 μc/flask in the absence of carrier acetate.

Application of this method of producing radioactive β-carotene to other fungi probably cannot be made without a thorough study of the species and isolates to be used.

ACKNOWLEDGMENTS

We wish to express our appreciation to Mrs. Ruthann Folmer, Mrs. Leela Zachariah, Miss Phyllis Vannoy, Mr. Charles Payne, and Mr. Fun Sun Chu for faithful technical assistance. We appreciate very much the kindness of Dr. C. D. Thomas, Head, Physics Department, in permitting us to use the facilities the isotope laboratory.

SUMMARY

A reliable method for producing and purifying radioactive β-carotene by an isolate of *Phycomyces blakesleeanus* in still culture is described in detail. Only a trace of carotene was produced during the early phase of rapid mycelial growth. Carotenogenesis became appreciable as the phase of rapid growth declined, and continued for 4 to 5 days after the production of mycelium nearly ceased. Conditions highly favorable for

growth or sporulation were unfavorable for the production of β-carotene. The carotene content of the mycelium reached 0.3 to 0.35 percent after 8 to 9 days of incubation. A 4- to 7-day-old culture grown on 25 ml of medium utilized as much as 12.2 mg of potassium acetate daily. Less glucose was utilized by cultures receiving added acetate than was utilized by the controls. When labeled acetate was added on the fifth day, radioactive β-carotene was synthesized. About one C^{14} atom out of 240 supplied as labeled acetate was recovered in crystalline β-carotene.

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THE GENERA OF THE DACRYMYCETACEAE[1]

LORENE L. KENNEDY[2]

The Dacrymycetaceae is a family of the Tremellales composed of a number of closely related species grouped together because of the possession of a remarkably uniform furcate basidium. The family is recognized as a well-founded taxon but there has been no agreement as to the limits of the genera and species. It is the purpose of this paper to present a classification of the genera based on a detailed study of the literature and the available collections of the species classified in these genera by other workers, supplemented, wherever possible, by study of fresh material.

A comprehensive survey of the literature on this family is given in the thesis (**1957**) upon which this paper is based and only limited reference will be made to it here. In 1791 Bulliard initiated the study of these fungi with a description of *Dacrymyces deliquescens* (as *Tremella deliquescens*) and Nees in 1816 established the genus *Dacrymyces* for one species, *Dacrymyces stillatus* Nees. This genus was recognized by Fries in 1822 with *Tremella deliquescens* Bull. cited as the type species. However, our real understanding of the group begins with Tulasne (**1853**) who was the first to emphasize the fundamental nature of the hymenial elements and to associate these fungi definitely with the Tremellales. Brefeld (**1888**) went only a step further in that he gave the group its family name listing *Calocera, Dacrymyces, Dacryomitra* and *Guepinia* as members. Coker (**1920**) made the first serious attempt to classify the genera in the Dacrymycetaceae, recognizing six genera based mainly on external features. Neuhoff (**1936**), maintaining that the genera are connected through transitional forms, combined most of the genera into the genus *Dacrymyces*, recognizing only *Dacrymyces* and *Calocera*. Brasfield (**1938**) defined seven genera and his treatment illustrates the value of small genera in providing a usable key. Kobayasi (**1939**) studied many of the genera very thoroughly and provided

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much information on the hyphal structure of the species, pointing the way toward the use of hyphal features in setting generic limits. Martin (**1952**) gives the most recent and comprehensive key to the Dacrymycetaceae.

In the attempts that have been made to classify these fungi practically every characteristic they possess has been described. As a consequence, the approach to the problem that remained was to combine and recombine these features in what it is hoped will be a better pattern of generic definition. These fungi are so simply constructed that all characteristics, both macroscopic and microscopic, must be utilized. Experience has taught that a pattern must be made for each genus and species, and one cannot say that any given feature is more reliable than another in the classification of these organisms. Since Neuhoff's combining of the genera did not produce a satisfactory scheme of classification, I adopted the policy of keeping any genus that could be defined with reasonable precision. Both Neuhoff (**1936**) and Kobayasi (**1939**) speak of species intermediate between the genera. The genera are indeed closely related but I am of the opinion that the following generic definitions allow satisfactory placement of the species that, in my experience, belong in this family. It is likely that this classification will be modified in the future, for developmental studies of the species are very rare as yet, but our present knowledge seems to warrant the recognition of nine genera: *Arrhytidia, Cerinomyces, Calocera, Dacrymyces, Dacryopinax, Ditiola, Dacryonaema, Femsjonia* and *Guepiniopsis.*

METHODS

It appears that the technique for the study of these fungi has been thought too simple to merit serious consideration in publications. To my knowledge, only one investigator, Martin (**1934**) has described how he studied his material, and no one has defined the terms used in the descriptions. I believe that both these subjects are important, particularly to those wishing to use the keys. This discussion deals first with the preparation of the material for study under the headings macroscopic features and microscopic features, and then with definition of terms.

MACROSCOPIC FEATURES. The basidiocarps were soaked in distilled water just long enough to swell and soften them without allowing loss of color. The color, shape, size and consistency described for the basidiocarp, except where the dry condition is indicated, refers to the condition of these features after the above treatment, and under the magnification of × 10–20.

It should be said here that if the material is fresh, or only a few months old, an attempt should be made to secure a spore print. This is done by placing the soaked basidiocarp with the hymenium facing downward against black paper and wrapping it in moist newspaper followed by a damp towel. If the material is viable, spores will be shed within 24 to 48 hours. Despite repeated urgings by such students of the Tremellales as Martin (**1952**), few collectors get a spore print when the collection is made. Such a spore print ensures that one has mature basidia and basidiospores.

MICROSCOPIC FEATURES. In preparing the material for microscopic study the soaked basidiocarp was treated in one of two ways. Sometimes it was cut longitudinally with a razor blade into sections that could be handled in pith. Then one of these sections was placed in pith and oriented so that thin, longitudinal sections could be cut. It was found that a hand microtome facilitated this operation and a straight razor was required. Such sections were used to study the organization of the hyphae in the more complex basidiocarps. At other times, particularly with small, undifferentiated basidiocarps, a small fragment including some of the hymenium was removed by means of a wedge-shaped needle and studied. In either case material was placed on a slide, wet with a drop of absolute alcohol which was quickly removed with absorbent paper, then mounted in a drop of 3% KOH to which were added 2 drops of phloxine stain (approximately 0.5 gms per 100 ml water), and a coverslip. Unless the material is fresh it should remain in the stain several minutes. The mixture of KOH and phloxine is then removed by absorbent paper and replaced by KOH. If it is necessary to see detail of the elements then it is advisable to tap out the material to separate the individual components.

Where the hyphae are described as possessing clamp-connections these are numerous, conspicuous and easily seen under the high power of the microscope (magnification of approximately × 400). If the hyphae are described as septate then they possess septa without clamp-connections, septa with collapsed clamp-connections or bulbous swellings, or the clamp-connections are obscure under high power. It is sometimes a problem to distinguish between true thick-walled hyphae and hyphae in which the walls have become strongly gelatinized, which may happen in older basidiocarps. The thick-walled hyphae of such genera as *Ditiola* have evenly thickened walls suggestive of fibers. The gelatinized hyphae have an irregularly wide, outer, colorless portion which does not stain with phloxine. Remarks regarding the thickness of hyphal walls refer to the appearance of the individual hyphae when

stained. The gelatinous matrix in which these hyphae are usually embedded does not stain and is therefore invisible. In the type of surface there is a gradation from the very rough through to the smooth. Where hyphae have been described as rough this feature is evident under high power.

Comments on the use of basidial measurements which are given in Kennedy (**1956**) apply equally well to all species. Except in a few cases, where the probasidia were so small that it was difficult to make out the basal septum, probasidia were measured under high power. Probasidial length has proved of little value in generic or specific delimitation owing to the overlapping limits of variation between species. However, a constant relationship was found between spore length and length of probasidia. In the collections of nearly all species studied, the ratio of probasidial length to spore length was found to be approximately 3:1. Thus if the collection lacks basidiospores, measurements of probasidia will give an indication of spore size. This will at least serve to reduce the number of possible species with which the collection could be identified.

In the description of the basidiospores the color in mass is the color of a fresh spore print. The number and kind of septa were observed in spores from a spore print or when the spores had begun to germinate, wherever possible. Spore measurements were made of spores from a spore print or of spores which had the number of septa possessed by germinating spores. All spores were measured under oil at a magnification of approximately × 900–1000. The routine practice was to measure ten spores, excluding abnormal ones, and give the range found. Where there was a question of distinctness of septa of spores, then the remarks refer to the appearance under high power.

The terms used in descriptions of the Dacrymycetaceae are listed in the following glossary and defined so as to explain my application of them to these fungi. Only those terms are included whose meaning might be open to question. In connection with basidial terminology in general, attention may be drawn to a recent discussion by Martin (**1957**). I have chosen to follow Neuhoff's terminology as redefined by Martin for the dacrymycetaceous basidium.

GLOSSARY

Amphigenous—hymenium borne on all sides of the basidiocarp except the part directly attached to or in contact with the substrate.

Applanate—flattened and horizontally expanded, maintaining this condition when moist.

Arthrospore—an imperfect spore formed by the breaking up of a hypha into separate sections. (This is considered a better term than oidium for the imperfect spores of *Dacrymyces deliquescens.*)

Coalescence—fusion between two or more basidiocarps or hymenial areas.

Confluent—coming or running together by irregular extension of hymenial areas.

Conidia—small, imperfect spores produced by some basidiospores upon germination.

Cortical hairs—surface outgrowths on the stipe or sterile portion of the pileus which are visibly different from the internal hyphae.

Cupulate—hymenium lining the interior of a cup-shaped basidiocarp or pileus, the outer surface of the cup being sterile.

Dicaryophysis—a sterile hymenial element narrower than the basidium, aseptate or septate, sometimes with clamp-connections, finally as long as or longer than the basidium. (These elements often do not develop fully until the basidia collapse, and they persist a considerable length of time. They stain like basidia.)

Early-septate spores—the condition in which numerous septate spores are found in a preparation from early stages.

Epibasidium—an extension of the probasidium upon which a sterigma and spore are borne.

Erumpent—bursting through the surface of the bark.

Erumpent from the wood—the condition where the basidiocarp breaks out of the wood and leaves a lens-shaped hole when it is removed from the wood, or when it falls out.

Germ-tube germination—where a tube-like hypha is produced from the basidiospore or one of its sections.

Heterogeneous—a basidiocarp composed of two kinds of hyphae exclusive of radicating base or cortical hairs.

Homogeneous—a basidiocarp composed of one kind of hypha exclusive of radicating base or cortical hairs.

Hypobasidum—the lower part of the basidium after it has begun to produce epibasidia.

Pezizoid—plate-like or cupulate but with a determinate margin.

Probasidium—the basidium before and as epibasidia are beginning to form. Its length is the distance between the basal septum and the tip of the central axis when epibasidia are just beginning to form.

Pustulate—basidiocarps which are blister-like or become so when moist.

Radicating base—a stipe-like part of the basidiocarp which passes through the bark and penetrates the wood below.

Resupinate—flat on the substratum, with the hymenium on the exposed side.

Stipitate—with a distinct head or pileus and stalk, free of the wood or bark.

Subiculum—a coarse mycelial base, more or less continuous over the substrate, upon which hymenial areas are formed.

Tardily-septate spores—the condition in which the majority of spores in a preparation are continuous, except in fully mature basidiocarps.

Unilaterial-inferior—hymenium borne on the under surface of a spathulate, petaloid or flabellate basidiocarp.

Wood—to be described as angiosperm (with vessels, fibers, etc.) or gymnosperm (with tracheids, bordered pits, lacking vessels).

DACRYMYCETACEAE Bref. Unters **7**: 138. 1888.

(*Caloceraceae* Pat. Essai Tax. Hymén 28. 1900.)

Basidiocarp effused, applanate, pustulate, cylindrical-attenuate or stalked and pileate, gelatinous or cartilaginous and drying horny or waxy, rarely arid; basidium at first cylindrical, then clavate, becoming furcate from the development of two extensions or epibasidia, each of which bears a spore on a sterigma; spores commonly curved-cylindrical, rarely subglobose to oval, usually becoming septate on germination and producing germ tubes or conidia.

The Dacrymycetaceae is distinguished from all other families of the Tremellales by the remarkably uniform furcate basidia with two sturdy epibasidia each tipped by a sterigma and a spore.

All the fungi classified in this family are saprobes on wood.

The TYPE genus is *Dacrymyces* Fries (Syst. Myc. **2**: 228. 1822).

The following key to the genera is a modification of the most recent classification of the family given by Martin (**1952**):

KEY TO THE GENERA OF THE DACRYMYCETACEAE

1. Originating as fertile patches on a loose subiculum, lacking a definite point of attachment; arid to waxy; changing little on soaking.....(1) *Cerinomyces*
1. Originating as pustules, discs or cylinders attached individually to the substrate; horny when dry, swelling and becoming gelatinous or cartilaginous on soaking.....2
   2. Heterogeneous (exclusive of rooting base and cortical hairs) with a region of thin-walled, branching hyphae next the hymenium and thick-walled, fibrous hyphae in the stalk.....(2) *Ditiola*
   2. Homogeneous (exclusive of rooting base and cortical hairs).....3
3. Cylindrical-attenuated, simple or branched; in cross section a central core of compact hyphae surrounded by a zone of loosely interwoven hyphae enclosed in turn by the hymenium.....(3) *Calocera*
3. Pustulate, discoid, pezizoid, stipitate and pileate, spathulate or petaloid; not zoned in cross section.....4
   4. Stipitate and spathulate, obliquely cupulate or petaloid; hymenium finally unilateral and inferior (pileus occasionally lobed or somewhat morchelloid with hymenium appearing amphigenous but composition homogenous of thick-walled, fibrous hyphae with bulbous septa).....(4) *Dacryopinax*
   4. Pustulate, discoid, pezizoid or stipitate and pileate; hymenium amphigenous, plane, concave or lining the interior of a cup.....5
5. Hymenium pruinose or farinaceous; stalk cartilaginous, becoming dark-brown and varnished; sterile stalks frequent.....(5) *Dacryonaema*
5. Hymenium gelatinous or waxy; stalk when present gelatinous, smooth or tomentose; sterile stalks absent.....6

6. Basidiocarp (exclusive of cortical hairs) composed of thick-walled hyphae.....(6) *Femsjonia*
6. Basidiocarp (exclusive of cortical hairs) composed of thin-walled hyphae....7
7. Cupulate on a constricted base; hymenium lining the interior of a cup; cortical hairs clavate or pyriform, often beaked, usually with basal clamp-connections, in a regular palisade layer.....(7) *Guepiniopsis*
7. Pustulate, discoid or applanate, sometimes slightly centrally depressed; cortical hairs, where present, clavate, never beaked, not in a regular palisade layer. Basidiocarp rarely cupulate but then stipitate with septate, clavate hairs and 7-septate spores.....8
8. Applanate, commonly confluent to form flat, resupinate layers; waxy; dull ochraceous to buff.....(8) *Arrhytidia*
8. Pustulate or pezizoid, stipitate or sessile; sometimes coalescing but not forming flat layers; gelatinous; never dull ochraceous to buff..(9) *Dacrymyces*

1. CERINOMYCES Martin, Mycologia **41**: 82. 1949.
Ceracea Auct. p.p.

Thin, ochraceous to buff-colored patches of hymenium on a loose subiculum; lacking a definite point of attachment to the substrate; arid to soft-waxy, changing very little on soaking; hyphae with conspicuous clamp-connections, scanty; basidiospores curved-cylindrical, aseptate or very tardily and obscurely 1-septate. Germination not observed.

TYPE: *Cerinomyces pallidus* Martin.

Martin (**1949**) defined this genus to include species formerly classified in the genus *Ceracea*, in which the basidiocarps lack any definite point of attachment and are arid to soft-waxy in consistency. Members of this genus are remarkably like a *Corticium* as far as macroscopic features are concerned, and would likely be identified as that genus unless the dacrymycetaceous basidia were observed. *Cerinomyces* is characterized by a basidiocarp in which the hymenium originates on a loose subiculum as ochraceous to buff patches which lack any definite point of attachment. That is, there are no pustules or discs attached individually to the wood at any stage of development, a feature found in other genera of the family. In addition, the consistency is arid to slightly waxy and there is no change, or very little, when dry specimens are soaked. When a section of the material is examined, the short, "stubby" basidia, the aseptate or very obscurely septate spores, and the scanty hyphae with conspicuous clamp-connections form a pattern not met with in other species of this family. Two species are known for this genus.

In connection with this genus it should be noted that Donk (**1956**) suggested that *Cerinomyces* be removed from the Dacrymycetaceae and the Tremellales and placed in the Homobasidiomycetes near *Corticium*.

In support of this contention he notes the arid consistency of the basidiocarp, the lack of rooting bases, the generally aseptate spores, the lack of production of conidia by the spores, and the so-called broadly clavate basidium.

On the basis of careful study of 14 collections of *Cerinomyces* species including the type I would disagree with Donk's proposal. It is true that the consistency of *Cerinomyces* is arid to somewhat waxy while other members of the family show a more or less gelatinous consistency. However, genera with basidiocarps having various kinds of consistency such as arid, waxy, gelatinous and fleshy are associated in such families of the Tremellales as the Tulasnellaceae and the Auriculariaceae, and this practice does not lead to a heterogeneous grouping when other features are considered. Since there are no individual basidiocarps in *Cerinomyces,* there can, of course, be no individual points of attachment to the wood, but this condition is not, in my opinion, of any great taxonomic significance at the family level, and can be met with in some of the Dacrymycetaceae that produce numerous basidiocarps which become effused and coalesced. The spores are generally aseptate in our collections, but spores with one septum have been observed, and since spore germination has not been seen, the possibility that the spores are very tardily septate and become so on germination cannot be excluded. In this connection it may be noted that the spores of *Dacrymyces punctiformis* Neuh. are very tardily septate and commonly appear aseptate. Moreover, the spores of some of the lower Homobasidiomycetes such as *Exobasidium* commonly become septate on germination. So far as the statement about production of conidia from basidiospores is concerned, Donk is voicing a generally held, but incorrect idea, that the basidiospores of the Dacrymycetaceae always germinate by the production of conidia developing from the spore sections. It has been found that the basidiospores of this family produce germ tubes just as often as conidia. For example, *Dacrymyces deliquescens* (Mérat) Duby and *Dacrymyces palmatus* (Schw.) Bres. commonly exhibit both kinds of spore germination, sometimes in the same preparation, while *Ditiola radicata* Fries generally produces germ tubes and rarely conidia.

The points just discussed are believed to carry some weight in the question of classifying *Cerinomyces,* but in the classification of the Basidiomycetes the form of the basidium is considered the fundamental feature. Donk said, "In *Cerinomyces* the young basidia are too broadly clavate to be identical with those of the Dacrymycetaceae." I cannot accept this statement. The basidia of *Cerinomyces* are long-cylindrical in shape, 3–4 μ in diameter throughout before epibasidia form, just as

those of other members of the family. The only difference is that they are usually notably shorter. However, some of the collections of *Dacrymyces minor* Peck showed basidia of the same proportions as those of *Cerinomyces*. When the epibasidia are formed in *Cerinomyces* they have the same sturdy proportions of those of other dacrymycetaceous species, and are tipped by a short sterigma. They would not be mistaken for sterigmata of a homobasidium. In view of these facts I consider *Cerinomyces* belongs in the Dacrymycetaceae.

2. DITIOLA Fries, Syst. Myc. **2**: 169. 1822.
Dacryopsis Massee, Jour. Myc. **6**: 182. 1891.
Dacryomitra Auct. p.p.

Basidiocarp at first turbinate or patellate, finally stipitate and pileate; rooted in and erumpent from the wood; hymenium amphigenous, originating as a small disc which remains plane or becomes centrally depressed or convoluted; tough-gelatinous; composition heterogeneous, exclusive of rooting base and cortical hairs, with a zone of thin-walled, branching, many-septate hyphae adjacent to the hymenium and thick-walled, fibrous hyphae with few septa, lying more less parallel, in the basal portion or stalk; basidiospores curved-cylindrical, 1–3-septate, germination by germ tube or conidia.

TYPE: *Ditiola radicata* Fries.

Fries described this genus to include the single species *Ditiola radicata* and since the generic description is practically the same as the specific description the validity of the genus has been questioned. Furthermore, in this and many subsequent descriptions of the species, the external features of the presence of stipe and rooting base have been stressed as the important specific characters. This has led some workers such as Bourdot and Galzin (**1928**), Donk (**1931**) and Neuhoff (**1936**) to include *Ditiola radicata* in the genus *Dacrymyces*, as there are species of *Dacrymyces* which may have stipitate basidiocarps, and also *Ditiola radicata* may exhibit basidiocarps which are practically sessile but yet are producing mature basidia and basidiospores. It has also caused confusion between the genus *Ditiola* and the genus *Dacryomitra*, whose main characteristic is the presence of a stipe and pileus. Thus the three genera *Ditiola*, *Dacrymyces* and *Dacryomitra* have become entangled and species have been transferred from one genus to another at various times. Much of this confusion would have been avoided if Lindau's paper (**1894**) had been consulted. In this morphological study of the species *Ditiola radicata* he makes it clear that this species is not only a good species but sufficiently distinct from any species in the family to

justify a separate genus. Kobayasi (**1939**) is the only recent worker who has understood and fully described the genus *Ditiola* and in it he places *Ditiola radicata* and *Ditiola nuda* Berk. & Br., Ann. Mag. Nat. II **2**: 267. 1848. His work and that of Lindau were confirmed by a study of the collections in the S.U.I. herbarium.

The genus *Dacryopsis* Massee was described as distinct from *Ditiola* because of the production of so-called gonidiophores before basidia were formed. No one has been able to confirm the presence of these structures and it is generally considered that *Dacryopsis* is not a valid genus. It is difficult to identify Massee's species with any certainty and the only one that has been generally recognized is *Dacryopsis nuda* (Berk. & Br.) Massee, based on *Ditiola nuda* Berk. & Br. The original description suggests a *Ditiola* but one could not be sure of the species. However, the authors evidently knew of *Ditiola radicata* for they said, "This pretty species has the habit of *Ditiola radicata* but does not root in the wood nor has it any veil." It seems reasonable to consider these two species synonymous. All collections determined as *Dacryopsis nuda* possessed features that would place them in *Ditiola* as described above. The same lag in basidiocarp development exists so that nearly sessile basidiocarps may produce mature basidiospores.

In 1900 Patouillard transferred *Ditiola nuda* to the genus *Dacryomitra* Tul. and, although he gave no reason for this action, many authors have followed him in this treatment of the species. The many collections in the S.U.I. herbarium given this name all proved to belong in *Ditiola*, and were of the one species *Ditiola nuda*.

Examination of the type material of *Dacryomitra brunnea* Martin shows that this species also belongs in the genus *Ditiola*. It was interesting to find arthrospore formation in this collection and this may be the explanation of Massee's gonidiophores, for the species is closely related to *Ditiola nuda*.

Species of the genus *Ditiola* possess a tough-gelatinous basidiocarp which is rooted in and erumpent from the wood. A longitudinal section shows that the basidiocarp is heterogeneous with the part adjacent to the hymenium composed of thin-walled, branching, many-septate, loosely interwoven hyphae, while the stalk is constructed of thick-walled, compact hyphae with few branches and septa which tend to take a parallel course. Even where there is little external evidence of head and stipe these two zones may be recognized. There are species of the Dacrymycetaceae with thick-walled surface hairs, and others with a rooting base which may contain thick-walled hyphae, but only *Ditiola* is heterogeneous exclusive of rooting base and surface hairs. In *Ditiola* the stalk

often flares out at the top but the hymenium is essentially amphigenous. This feature, together with the heterogeneous composition, serves to distinguish members of this genus from other species of the family which occasionally, or constantly, develop a head and stalk.

Some fourteen species have been reported for the genus and in addition some species classified in other genera belong here, but there appear to be only two or three good species in this genus.

3. CALOCERA Fries, Elench. Fung. **1**: 233. 1828.
Caloceras Fries ex Wallr. Fl. Crypt. Germ. **2**: 534. 1833.

Basidiocarp cylindrical-attenuate, remaining simple or becoming branched; firm-gelatinous, drying horny; composition homogeneous of thin-walled hyphae, in cross section exhibiting a central core of compact hyphae surrounded by a zone of loosely interwoven hyphae enclosed in turn by the hymenium; basidiospores curved-cylindrical, becoming septate; germination by conidia or germ tube.

TYPE: *Clavaria viscosa* Fries, Syst. Myc. **1**: 486. 1821.

Since *Calocera* was described by Fries in 1828 the validity of the genus has never been questioned, for it is one of the few genera in this family with well-defined generic limits. The cylindrical-attenuate basidiocarp resembling that of a *Clavaria* and the furcate basidia have generally served to allow ready identification of collections as belonging to this genus without recourse to other features. The basidiocarp shows in cross-section an organization into three zones which is not found elsewhere in the family. This statement is based on study of *Calocera cornea* and *Calocera viscosa* collections supplemented by Brefeld's discussion of the genus in 1888. In *Dacryopinax spathularia* (Schw.) Martin there is an approach to this organization, at least in some of the collections, with a central core of parallel hyphae in the stalk surrounded by a zone of loosely woven hyphae. However, the hymenium is not regularly amphigenous in *Dacryopinax*. *Calocera* does not seem to present a problem of generic definition but the problem of specific limits is much in need of study. Saccardo lists some thirty-six species but it is likely that the number of good species is much smaller.

4. DACRYOPINAX Martin, Lloydia **11**: 116. 1950.
Guepinia Fries, Elench. Fung. **2**: 30. 1828 p.p.; not *Guepinia* Bastard 1812 (Cruciferae) nor *Guepinia* Fries 1825.
Dacryomitra Auct. p.p.

Basidiocarp at first discoid, becoming stipitate with an obliquely cupulate, spathulate, petaloid or, occasionally lobed and somewhat mor-

chelloid pileus, stipe and sterile part of pileus covered by a cortex of cylindrical hyphae with thick walls; hymenium unilateral, smooth, in gill-like folds or sometimes in lobes, inferior; tough-gelatinous to cartilaginous; composition homogeneous, of thick-walled fibrous hyphae with bulbous septa; basidiospores curved-cylindrical, 1–3-septate, germination by conidia.

TYPE: *Guepinia elegans* Berk. & Curt. Jour. Bot. & Kew Misc. **1**: 239. 1849.

Martin described this genus to include three species formerly classified in *Guepinia* Fries, a name not available for the fungi.

There is no difficulty in identifying collections as belonging to this genus if they contain a number of fully developed basidiocarps, for some will show the stipitate and spathulate, obliquely cupulate or petaloid form together with the unilateral inferior hymenium diagnostic for the genus. However, a stipitate and lobed or somewhat morchelloid phase with an apparently amphigenous hymenium can occur and, if growing isolated, might not be associated with *Dacryopinax*. Indeed, such forms have not been classified in the genus *Dacryopinax* but usually in the genus *Dacryomitra* Tulasne or occasionally in the genus *Dacryopsis* (*Ditiola*). The question of the relationship between the genus *Dacryopinax* and *Dacryomitra* is discussed under excluded genera.

5. DACRYONAEMA Nannf. Svensk. Bot. Tidskr. **41**: 336. 1947.

Basidiocarp at first a subcylindrical to conical puberulent stalk, which becomes resin-colored to almost black with a varnish derived from the agglutination of surface hairs; composition homogeneous, of thick-walled hyphae with very narrow lumina; pileus subglobose, farinaceous or pruinose, composed of radiating thin-walled hyphae of the hymenium; basidiospores curved-cylindrical, becoming septate; germination by conidia; sterile stalks frequent.

TYPE: *Dacryonaema rufum* (Fries) Nannf.

The single species is completely different from any other species of the Dacrymycetaceae in form and development. The small, cylindrical, brown, varnished, sterile stalks are most frequently encountered. The fertile basidiocarps bear a greyish, mealy head composed of hymenial elements. There is no question of the validity of this genus, which Nannfeldt described to contain the species *Dacryonaema rufum* which had been classified as a *Sphaeronaema* by Fries (**1823**) and as a *Sphaeronaemella* by Saccardo (**1884**).

6. FEMSJONIA Fries, Summa Veg. Scand. 341. 1849.

Basidiocarp at first pustulate, then pezizoid, sessile or on a short stalk; stipe and sterile part of the pileus with a white cortex composed of hyphae with thick gelatinized walls and clamp-connections at the septa, hymenium unilateral, superior; firm-gelatinous; composition homogeneous, of thick-walled hyphae which usually bear numerous clamp-connections but occasionally have bulbous septa; basidiospores curved-cylindrical, slowly 3-many-septate, germination by conidia.

TYPE: *Femsjonia luteoalba* Fries.

The description and notes given for this genus and its single species by Fries are unusually full, and, although he spoke of "globose basidia" there is no question of the identity of his species. In describing the genus Fries associated it with *Arrhytidia* Berk. & Curt., apparently considering *Arrhytidia* a cupulate form. He said, "*Femsjonia* although far more conspicuous is almost the same plant" (as *Arrhytidia*). This curious association of two such different fungi is explained, perhaps, by a collection labelled *Arrhytidia flava* Berk. & Curt. in the N.Y.B.G. herbarium. This collection, occurring on pine bark, was made in South Carolina by Schweinitz and determined by Curtis. Part of the collection accompanied by a photograph showed clearly that the species is *Femsjonia luteoalba.* If similar collections were distributed as *Arrhytidia flava* then one can understand this remark of Fries.

The descriptions of many European collections of *Femsjonia luteoalba* and those from Japan, as well as photographs such as those of Buller (**1922**) and Kobayasi (**1939**), suggest a thick, corky, turbinate to almost ungulate basidiocarp, with a plane, downward-facing hymenium. Such basidiocarps are superficially like those of *Ditiola radicata* Fries. The descriptions of American collections suggest a pezizoid basidiocarp on a short stipe which is firm-gelatinous but often collapses on the substratum. This is in agreement with the conception of Fries, who thought that *Peziza radiculata* Sowerby, which has a yellow, cupulate ascocarp, was the same species. The collections available for study mainly showed pezizoid basidiocarps of varying depth, either sessile or short-stipitate, which collapsed when old. One would not likely confuse them with *Ditiola radicata* but rather with *Guepiniopsis chrysocomus* (Fries) Brasf. or the stipitate and cupulate phase of *Dacrymyces palmatus,* both of which have multiseptate spores and thick-walled cortical hairs. Either this turbinate, corky type of basidiocarp is an early, though spore-producing stage in basidiocarp development, or else a slightly different form of the species.

Femsjonia luteoalba has been the only species of this genus generally recognized and it is the only one with which I am familiar. However, Kobayasi (**1939**) described a *Femsjonia orientalis* with yellow tomentum and smaller, 1–3-septate spores. On the basis of the material studied I consider this genus should be retained. There is no doubt *Femsjonia luteoalba* is a valid species, but it is difficult to assess its characters as to their value in generic distinction. In fully developed basidiocarps the internal hyphae, exclusive of cortical hairs, are thick-walled and this feature usually serves to separate the genus from some members of *Ditiola, Dacrymyces* and *Guepiniopsis*. The characteristics which seem of greatest practical value in identifying *Femsjonia luteoalba* are the large, slowly multi-septate spores, the numerous clamp-connections on the hyphae, and the type of cortical hairs, but whether these are only of specific value is difficult to judge. Study of additional collections of this species and of any other species assigned to the genus is needed.

7. GUEPINIOPSIS Pat. Tab. Anal. Fung. **1**: 28. 1883.
Heterotextus Lloyd, Myc. Writ. **7**: 1151. 1922.

Basidiocarps at first pustulate, becoming shallow-pezizoid or cupulate on a constricted base or a short stipe, usually rooted in the wood; hymenium lining the interior of the cup; firm-gelatinous; composition homogeneous, of thin-walled hyphae usually with conspicuous clamp-connections, sterile surface rough and covered with a regular palisade of clavate, pyriform or broadly cylindrical cortical hairs which, when fully developed, have thick, gelatinous walls, narrow lumina and rounded apices; basidiospores curved-cylindrical, becoming 3–7-septate, germination by conidia or germ tube.

TYPE: *Guepiniopsis tortus* Pat.

Patouillard described this genus as stipitate and cupulate with the hymenium lining the interior of a cup. *Guepiniopsis tortus* is described at this time as follows, "Height 10–15 mm, yellow or orange, stipe slender enlarging to a cup with a wavy margin, cup covered externally by longitudinal channels. . . . The hyphae of the external surface are forked and terminate by a swollen part cut off by a septum and hollow inside. Sometimes these swollen parts are formed in moniliform chains which may separate" (translation). One would expect this species to be cited as the type of the genus but Brasfield (**1938**) and Martin (**1952**) cite *Dacrymyces tortus* Fries, Elench. Fung. **2**: 36. 1828 as the type species for *Guepiniopsis* and as a synonym of their *Guepiniopsis torta* (Fries) Pat. Kobayasi (**1939**) believed also that this genus was based on *Dacrymyces tortus* Fries. Evidently these authors consider

that *Dacrymyces tortus* Fries is a synonym of *Guepiniopsis tortus* Pat. but Patouillard does not cite this species nor refer to it in any way.

The description of *Dacrymyces tortus* given by Fries in 1828 is scanty but does suggest a *Guepiniopsis*, as do his remarks relating it to *Peziza* and *Helotium* species. However, in 1838 Fries associated this species with *Dacrymyces stillatus* Fries, synonymous with *Dacrymyces deliquescens* (Mérat) Duby, and in 1874 with *Dacrymyces deliquescens* directly. Neuhoff (**1936**) remarked that *Dacrymyces tortus* Fries is the same as *Dacrymyces punctiformis* Neuh. and *Dacrymyces romellii* Neuh. described at the same time, on the basis of study of the type collection. Nannfeldt (private communication) stated that *Dacrymyces tortus* Fries, *Dacrymyces punctiformis* and *Dacrymyces romellii* are synonyms and thus confirmed Neuhoff's statement. Thus *Dacrymyces tortus* Fries cannot be cited as the type species of the genus *Guepiniopsis*, for it is a different species from *Guepiniopsis tortus* Pat.

Dennis (**1952**) examined specimens of *Peziza buccina* Pers. Syn. Fung. 659. 1801 from Persoon's herbarium and concluded that they represented, "clearly the species fully described by the Tulasnes under the name *Guepinia Peziza* and better known today as *Guepiniopsis torta* (Fries) Pat." Fries recognized *Peziza buccina* Pers. in 1822. Thus it appears that the correct name for the type species of *Guepiniopsis* is **Guepiniopsis buccina** (Pers. ex Fries) comb. nov., based on *Peziza buccina* Pers. ex Fries, Syst. Myc. **2**: 129. 1822.

Members of the genus *Guepiniopsis* are seldom difficult to recognize, for the pezizoid basidiocarp on a short constricted base or stalk, with the hymenium lining the inside of the cup and the outer surface covered with a palisade layer of broadly-cylindrical, thick-walled cortical hairs, is a structure not met with in the other genera of the family. The rare cupulate phase of *Dacrymyces palmatus* is somewhat similar but the cortical hairs are quite different and there are no clamp-connections on the hyphae. It would appear that *Femsjonia luteoalba* is the species most likely to be confused with species of *Guepiniopsis* but in *Femsjonia* the internal hyphae are thick-walled and the cortical hairs quite different in shape.

There are at least three species and possibly four which belong in this genus.

8. ARRHYTIDIA Berk. & Curt. Jour. Bot. & Kew Misc. **1**: 235. 1849.
Ceracea Auct. p.p.; not *Ceracea* Cragin 1884.

Basidiocarp applanate, originating as smooth, flattened discs or sometimes pustules, each attached to the wood by a radicating base,

frequently becoming confluent to form large, irregular layers up to several centimetres in extent, then often appearing broadly attached, pale ochraceous to buff with pink or cinnamon tints, drying dull orange, buff or reddish brown; hymenium amphigenous; waxy-gelatinous, occasionally tough-gelatinous; composition homogeneous, of thin-walled hyphae, usually with conspicuous clamp-connections; basidiospores curved-cylindrical, early 3-septate, germination by conidia or germ tube.

TYPE: *Arrhytidia flava* Berk. & Curt.

This genus has been linked constantly with *Ceracea* Cragin 1884. Martin (**1949**) showed that *Ceracea* Cragin was based on an imperfect fungus and proposed that the species heretofore assigned to this genus be assigned to the genera *Arrhytidia* and *Cerinomyces*. In this connection he said, "The concept of *Arrhytidia* here suggested is that, except for its firm-gelatinous or waxy texture, it is similar to *Dacrymyces* in its earlier stages, beginning as a group of rooted, pustular, discoid fructifications which soon anastomose and eventually form a netted or more or less continuous film on the substratum." *Arrhytidia* was initially described as follows: "Hymenophore formed from a mold-like mycelium, which forms a margin, surface of the hymenium soft-waxy, smooth without folds, spores oblong." As might be expected there has been no agreement on the limits of this genus and the concept has been most difficult to apply in identification of specimens. Furthermore, the genus has come to include a heterogeneous collection of species in which the form of the basidiocarp more or less agrees with the above description at some stage in its development. Most authors have laid more emphasis on the coalescence of pustules than on any other feature, although this is not mentioned in the original description. Authors such as Lloyd (**1920, 1921, 1928**), Coker (**1920, 1928**), Bresadola (**1911**) and Brasfield (**1938**) express doubt as to the distinction of *Arrhytidia* and *Ceracea* (broad sense) from the genus *Dacrymyces*, while Neuhoff (**1936**) and Kobayasi (**1939**) mention neither *Arrhytidia* nor *Ceracea* in their publications on the Dacrymycetaceae.

Examination of some forty-three collections determined as species of *Arrhytidia* or *Ceracea*, supplemented by a review of the literature descriptions of species assigned to these genera, showed that these species fall into two groups. In the larger group the basidiocarps are, in general, dull ochraceous to buff in color and waxy-gelatinous in consistency and form corticioid plaques, applanate or flattened layers, with or without a mycelial margin, rooted or broadly attached to the substratum. This group might be designated the *Arrhytidia involuta* group and, with many authors, would include species assigned to *Cerinomyces* by

Martin. In the second group the basidiocarps are dark, chestnut-brown to black, convoluted, tough-gelatinous pustules attached by a point, which often form sheets by coalescence but retain evidence of pustular origin. This group comprises the species *Arrhytidia enata* as understood by Coker (**1920**). The basidiocarps of these two groups have in common only the tendency to form large irregular masses through fusion of a number of basidiocarps and the presence of clamp-connections on the internal hyphae. They differ in color, form, consistency, presence of dikaryophyses and spores.

Since *Arrhytidia flava*, certainly very similar to *Arrhytidia involuta*, and considered a synonym by Coker, is the type of the genus *Arrhytidia*, it is difficult to understand why Coker (**1928**) placed *Tremella enata* Berk. & Curt. in this genus. I consider that *Tremella enata* belongs in the genus *Dacrymyces* where it was placed by Massee (**1891**). Where there are only a few separated basidiocarps the species would immediately be classified as a *Dacrymyces*. Where there are many, crowded basidiocarps, fusion may take place, producing the large masses which led Coker to consider it an *Arrhytidia*. However, collections with numerous basidiocarps and no coalescence have been found, and certainly the consistency is not in the least waxy. Of greatest importance is the fact that whatever the macroscopic features of these basidiocarps the microscopic features were the same in all. In every case dikaryophyses with irregular, branching apices which project beyond the basidia were present and the spores were very tardily 3-septate.

It might be noted here that the fusion of crowded basidiocarps, even to the point where individual margins have practically disappeared has been found in species of *Dacrymyces*, especially *Dacrymyces deliquescens*. Moreover, the feature of a white, fimbriate margin so often listed as characteristic of the genus *Arrhytidia* may be met with in any genus of this family in young stages. It appears to be due to the occasional persistence of the mycelial weft of hyphae from which the basidiocarp originated.

In the *Arrhytidia involuta* group some of the collections belonged in *Cerinomyces* while the majority of the remainder could be identified as *Arrhytidia involuta* (Schw.) Coker. Lowy (**1956**) has given a good macroscopic description of this species, "Fruiting bodies resupinate, forming small, irregular, thin, rust-colored flake-like patches when dry." Since this species is very different from any other member of the family I consider the genus *Arrhytidia* should be maintained. For the present the genus will have to be interpreted on the basis of *Arrhytidia involuta*, the only species I should care to list with certainty.

The genus may be recognized by the pale ochraceous to buff, applanate basidiocarps each attached by a radicating base, which often become confluent to form large, irregular layers. The consistency is usually waxy-gelatinous but occasionally tough-gelatinous. It may be distinguished from *Cerinomyces* by the manner in which the basidiocarps arise. In *Arrhytidia* they originate as pustules attached individually to the substrate and, even when extensive fusion has taken place, the pustular origin is still evident and often the rooting bases also. The color, form and consistency serve to separate *Arrhytidia* from *Dacrymyces,* with which it has often been confused.

Although *Arrhytidia involuta* is the only well known species it appears that there are several other species which belong in this genus. Studies of these species as well as other collections determined as species of *Ceracea* are needed before an idea of the number of species belonging to this genus can be gained.

9. DACRYMYCES Fries, Syst. Myc. **2**: 28. 1822.
Septocolla Bon. Handb. Allg. Mykol. 152. 1851.

Basidiocarps originating as pustules, sessile, and pulvinate, turbinate, discoid and somewhat depressed centrally, flabellate or stipitate and pileate with a spathulate, discoid or convoluted pileus, plane, slightly convoluted to cerebriform, often coalescing to form irregular masses or raised, erumpent clusters, but always retaining evidence of pustular origin, attached by a point, a short stalk or a tough, radicating base which passes through the bark and penetrates the wood below, yellow, orange or dark brown in color; soft to tough-gelatinous; hymenium amphigenous, rarely unilateral and superior; composition homogeneous, of thin-walled hyphae, exclusive of radicating base or cortical hairs; basidiospores curved-cylindrical (in one species oval), becoming septate, germination by germ tube or conidia.

TYPE: *Tremella deliquescens* Bull. Hist. Champ. France 219. 1791.

Nees established this genus in 1816 for the species *Dacryomyces stillatus* Nees and in 1822 Fries recognized the genus, citing *Tremella deliquescens* as the type species.

Members of the genus will show a pattern composed of the following features. The basidiocarps arise as pustules attached individually to the substrate, are gelatinous, swelling when moistened, and are colored some shade of yellow, orange or brown. The hymenium is regularly amphigenous and the composition is homogeneous, of thin-walled hyphae, exclusive of radicating base and cortical hairs. The internal thin-walled

hyphae serve to separate *Dacrymyces* from *Ditiola* and *Femsjonia*. The position of the hymenium differentiates *Dacrymyces* from *Dacryopinax* and *Guepiniopsis*. The origin, color and consistency differentiate *Dacrymyces* from *Arrhytidia* and *Cerinomyces*, while external shape and lack of zonation in cross section separate the genus from *Calocera*. Basidiocarps of some species belonging to other genera may go through a pustule stage which produces normal basidiospores, and identification of collections of such stages might be sought for in the genus *Dacrymyces*. Generally, however, these collections will show some feature which does not fit the *Dacrymyces* pattern, as, for example, almost sessile *Ditiola* basidiocarps which will show the heterogeneous composition.

On the basis of these studies eight species have been recognized. It is likely that several more valid species exist, but certainly not the 116 described.

EXCLUDED GENERA

1. *Dacryomitra* Tulasne, Ann. Sci. Nat. V. **15**: 217. 1872.

This genus was based on *Dacryomitra pusilla* and the description of the basidiocarp reads in part, "forma autem minimarum *Typhularum* seu *Mitrularum*, 8–10 millim. altus, rectus et rigidulus e stipite gracili, tereti, semipellucido levique, et clavula coloris nonnihil opacioris, ovato-conica, continua, 4–5 millim. longa et 1.5–2 mm crassa." Tulasne did not give a formal generic description and these remarks have apparently formed the basis of the accepted concept of the genus. Most authors have considered that the important feature is the presence of a stipe and head and so this genus has come to contain many species which possess stipitate and pileate basidiocarps at some stage of development, regardless of other features. Since a number of species in this family may show a complete range from sessile to stipitate and pileate basidiocarps, and since any of these stages may produce typical basidiospores, it was inevitable that *Dacryomitra* should contain a heterogeneous group or species.

I have not seen the type collection but the rest of the unusually full description suggests a *Dacryopinax* to me. At any rate, study of available collections of species assigned to this genus has presented convincing evidence that *Dacryomitra* is a genus composed of species belonging to other genera. It has been found that *Dacryomitra nuda* (Berk. & Br.) Pat. and *Dacryomitra brunnea* belong in the genus *Ditiola*. *Dacryomitra stipitata* (Peck) Burt (*Dacryomitra ceracea*

(Coker) Brasf.) is a phase of *Dacryopinax spathularia*. Collections of these two species agree in microscopic features and substrate and show variation only in basidiocarp shape. Moreover, several large collections identified as *Dacryomitra stipitata* and *Dacryopinax spathularia* have included both spathulate basidiocarps with a unilateral, inferior hymenium and stipitate and pileate ones with a more or less amphigenous hymenium. This conclusion is supported by Bodman's paper (**1938**) on *Guepinia spathularia* (*Dacryopinax spathularia*), and comments on the species by Coker (**1920**), Brasfield (**1938**) and Olive (**1948**). *Dacryomitra ramosa* Wehmeyer and *Dacryomitra depallens* Lloyd are phases of *Dacrymyces palmatus*. Martin (**1948**) says that *Dacryomitra glossoides* Bref. is probably *Dacryopinax fissus* (Berk.) Martin and the available collections of this species belong in *Dacryopinax*.

2. *Dicellomyces* Olive, Mycologia **37**: 544. 1945.

This genus includes a single species, *Dicellomyces glocoporus*, parasitic on the leaves of *Arundinaria tecta*. Nannfeldt (**1947**) remarked that this genus differs so much from the rest of the Dacrymycetaceae that it may eventually be excluded from that family. The most important character which sets *Dicellomyces* apart from members of the Dacrymycetaceae is the basidium. It has a basidium which consists of a swollen basal part that seems to be a persistent probasidium and a long, narrow region from which develop two rather thick sterigmata. Such a basidium is quite different from the very constant, furcate basidium of the Dacrymycetaceae and is the kind described for some members of the Corticiaceae or Exobasidiaceae by Gäumann (**1922**) and Neuhoff (**1924**). Furthermore, the spores are shed in pairs or clusters and lack an apiculus, and *Dicellomyces* is a parasite while all known members of the Dacrymycetaceae are saprobes.

SUMMARY

Nine genera are described for the Dacrymycetaceae and a key is provided for their identification. A section dealing with the preparation of the material for study and the application of terms to these fungi is included.

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THE GENUS DACRYMYCES [1]

LORENE L. KENNEDY

A key to the genera of the Dacrymycetaceae and a taxonomic discussion of the various genera, including *Dacrymyces,* may be found in the preceding paper (Kennedy, **1958**). There the methods employed in the study of these fungi and the terms used in the descriptions were explained.

When Nees established the genus, which he spelled *Dacryomyces,* in 1816, he described the sporocarp as a fleshy or gelatinous substance, round or discoid in form, bright yellow or red in color and composed of interwoven filaments with spores. It included one species, *Dacryomyces stillatus.* Fries, in 1822, added to the description the characteristics of homogeneous consistency and spores formed on all sides of the sporocarp. Since then the boundaries of the genus have exhibited great flexibility, expanding or contracting according to the number of other genera recognized for the family. For example, in Neuhoff's (**1936**) treatment *Dacrymyces,* while not defined, includes at least species belonging to the genera *Ditiola, Guepiniopsis* and *Femsjonia,* and one gains the impression that he would place species of nearly all the genera but *Calocera* there. On the other hand Martin's (**1952**) concept is much narrower, because of the recognition of ten other genera in the family. The concept of the genus presented in this paper was arrived at by defining eight other genera for the Dacrymycetaceae. Such a procedure leads to a view of the genus *Dacrymyces* which is somewhat negative in nature, for one thinks of it as a group of species that does not fit the pattern of the other, more easily defined, genera. Thus we find that, except for allowance of considerable variation in external basidiocarp form, the present description differs little from that of Fries. *Dacrymyces* still includes the largest number of species but seems now to comprise a natural group.

[1] Based on Part II of a thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the State University of Iowa, August, 1957. I wish to express my gratitude to Professor G. W. Martin for his guidance during the course of this study.

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In the following treatment I have extended the concept of the genus as described by Martin (**1952**) to include part of the genus *Arrhytidia* and some stipitate forms formerly classified in the genus *Dacryomitra*. There have been no new species described but the scope of many of them has been considerably broadened. The overlapping limits of variation of many characteristics possessed by these species, and the existence of intermediates, blur the specific limits and make classification difficult. Numerous examples illustrating this situation have been described by Burt (**1921**), Neuhoff (**1936**), Bourdot and Galzin (**1928**), Kobayasi (**1939**), Olive (**1947, 1953**) and others. However, these 'atypical' collections have usually been forced into existing specific categories by the taxonomist, even though he may acknowledge them in comments following formal species descriptions. It is believed that the existence of these phases should always be indicated in species descriptions and, most important, in the key to the species, wherever possible.

If this policy is adopted then one must decide how to deal with these difficult phases in the keys and species descriptions. So far as truly intermediate collections are concerned, the only recourse is to describe them in the notes of the associated species. The apparently stable varieties or phases which are related so closely that separation into species is not feasible may be included in the description of the species concerned or named as varieties. The first course has been adopted when the broadening of the species description to include such variations does not result in excessive qualification of characteristics, so that a reasonably clear species concept can be maintained. This was the case with *Dacrymyces palmatus* and *Dacrymyces punctiformis*, to give two examples. Where extending the species description to include these variations would result in a species most difficult to comprehend, I have given them the rank of variety. An example of this procedure is the treatment of *Dacrymyces deliquescens*. These varieties have been included in the key.

A number of species have been reduced to synonymy where adequate material was available to justify this action. Where I have seen no specimens I have suggested possible identities.

The basidiocarps of all species discussed in this account have been found on the bark or exposed wood of seed plants. These studies show that the taxonomic character of type of substrate should be relegated to a subordinate position in *Dacrymyces* species descriptions. Except in a few instances, and these may well be due to insufficient collections, these saprobic fungi appear not to be limited to wood of a given kind or condition (that is, whether the bark is present or absent). However, it is

sometimes possible to say that a species is more frequent on a given kind of wood. Our knowledge is insufficient to give us an accurate picture of the world distribution of the *Dacrymyces* species. Collections examined have come from nearly every state in the United States, from Brazil, Canada, Colombia, England, Germany, Greece, Hawaii, Latvia, the Netherlands, Panama and Sweden. In addition, there have been reliable reports from Australia, China, Finland, France and Japan. It appears that species of this genus are cosmopolitan, and it is probable that they are much better represented in tropical and Asian countries than available collections or reliable reports would indicate. Symbols for Herbaria are taken from the Index Herbariorum, Lanjouw and Stafleu, 1956.

Since the limits of the genus *Dacrymyces* have been so nebulous the usual duplication of names has resulted. In the Species Inquirendae section of the thesis forming the basis of this paper all the *Dacrymyces* names known to me are listed together with available information about them.

As a full generic description was given when the family was discussed, only a shortened description is set forth here.

DACRYMYCES Nees ex Fries, Syst. Myc. **2**: 228. 1822.
[*Dacryomyces* Nees, Syst. Pilze Schw. 89. 1816.]
Septocolla Bon., Handb. allg. Mycol. 152. 1851.

Basidiocarps originating as pustules attached individually to the wood, sessile or becoming stipitate and pileate, often coalescing to form irregular clusters, yellow, orange or dark brown in color; gelatinous; hymenium amphigenous; composition homogeneous of thin-walled hyphae, exclusive of radicating base or cortical hairs; basidiospores curved-cylindrical (in one species oval), becoming septate.

TYPE: *Tremella deliquescens* Bull. Hist. Champ. France 219. 1791.

KEY TO THE SPECIES

1. Internal hyphae with numerous, conspicuous clamp-connections.....2
1. Internal hyphae septate or with few, obscure clamp-connections.....7
2. Spores subglobose to broad oval with cross and vertical septa.....
.....(1) *D. ovisporus*
2. Spores curved-cylindrical or allantoid.....3
3. Basidiocarps chestnut brown, drying dark brown or black; dikaryophyses with irregularly branched apices present.....4
3. Basidiocarps yellow or orange, drying amber; dikaryophyses simple.....6
4. Basidiocarps attached by a short stalk, discrete; spores becoming 3-7-septate with narrow septa, spores mostly 16.5–24 × 6 μ....(2) *D. nigrescens*

4. Basidiocarps attached by a point, usually becoming effused and coalescing to form large, irregular masses; spores 1-3-septate with narrow or wide septa, spores mostly 8–15 × 3–6 μ.....5
5. Spores tardily 1-septate, occasionally with 2 additional septa, septa narrow, 8–13 × 3–4.5 μ.....(3) *D. enatus* var. *enatus*
5. Spores early 3-septate, septa becoming wide and gelatinous, 13–15 × 5–7 μ.....(4) *D. enatus* var. *macrospora*
6. Spores curved-cylindrical to plump-allantoid, distinctly 3-7-9-septate, (10–)14–25 × 6–9 μ.....(5) *D. abietinus* var. *abietinus*
6. Spores cylindrical, slightly curved, indistinctly 1-3-septate (regularly undivided), (7–)10–15(–17) × 3–5 μ.....(7) *D. punctiformis*
7. Spores allantoid and very strongly curved, becoming multiseptate (15 or more); basidia with abruptly obtuse bases.....(8) *D. falcatus*
7. Spores curved-cylindrical or plump-allantoid, 3-7-septate; basidia with tapering, rounded bases.....8
8. Spores early and distinctly 7-septate, septa narrow; clavate cortical hairs with thick walls present on stalk and radicating base..(9) *D. palmatus*[2]
8. Spores usually 3-septate, septa indistinct, or distinct and wide, early or tardily formed; clavate cortical hairs absent.....9
9. Spores plump-allantoid, varying in length from 11–22 μ; usually some spores with more than 3 septa.....(6) *D. abietinus* var. *triseptatus*
9. Spores curved-cylindrical, varying in length 11–17 μ; none with more than 3 septa.....10
10. Basidiocarp greenish-yellow or amber, then dingy-yellow or orange; drying inconspicuous; scarcely coalescing; spores yellow in mass, finally 3-septate, usually on angiosperm wood.....(10) *D. deliquescens* var. *minor*
10. Basidiocarps orange-yellow or reddish-orange; drying conspicuous; frequently coalescing to form irregular masses, erumpent, or raised clusters; spores orange in mass, early 3-septate.....11
11. Spores distinctly 3-septate, walls and septa usually becoming wide and gelatinous; arthrospores in the basidiocarp or in separate sporocarps (rarely absent); lacking radicating bases; hyphae smooth; on gymnosperm or angiosperm wood.....(11) *D. deliquescens* var. *deliquescens*
11. Spores distinctly or indistinctly septate, walls and septa narrow, arthospores absent; attached by a radicating base or short stalk; some hyphae rough (rarely all smooth); often in raised clusters; commonly on angiosperm wood.....(12) *D. deliquescens* var. *ellisii*

1. DACRYMYCES OVISPORUS Bref. Unters. **7**: 158. 1888.

Basidiocarp pale orange, drying dark brown and conspicuous, pustulate and convoluted; firm-gelatinous; rooted in the wood; 2–5 mm diameter; hyphae smooth, thin-walled, with numerous, conspicuous clamp-connections; probasidia (58–)61–70(–83) × 5–6 μ with basal clamp-connections; dikaryophyses with clamp-connections and irregularly shaped apices, up to 67 μ in length; basidiospores subglobose to broadly

[2] Martin in this issue (Mycologia **50**: 939) describes a new species *Dacrymyces dictyosporus* from Honduras that differs from *D. palmatus* in the possession of larger spores with longitudinal as well as transverse septa.

oval with 3–5 cross and vertical septa, apiculate, (9–)14–15 × 8–11 μ, producing spherical conidia.

TYPE LOCALITY: Germany.

HABITAT: Gymnosperm wood.

ILLUSTRATIONS: Brefeld Unters. **7**, *pl. 10, f. 20–21.*

Specimen examined: Sweden, *Berit and John Eriksson 2269,* (1A).

The spores in this species are completely different from those of any species classified in the Dacrymycetaceae. The species is apparently rare, having been reported once from Germany and once from Sweden. It has not been found on this continent.

2. DACRYMYCES NIGRESCENS Lowy, Bull. Torrey Bot. Club **81**: 300. 1954.

Basidiocarp chestnut brown with pink tints to very dark brown, drying black and conspicuous, pustulate and strongly convoluted, erumpent and attached by a pallid radicating base to the wood, 4–5 mm in diameter; tough-gelatinous; hyphae smooth with somewhat thickened, gelatinous walls and numerous, conspicuous clamp-connections; probasidia with wide basal septa, (57–)61–74 × 4–6 μ accompanied by dikaryophyses (with clamp-connections) which sometimes have irregularly shaped apices and usually project beyond the basidia; basidiospores plump-allantoid, strongly apiculate, tardily 3–7-septate, (10.5–)16.5–24 × (3–)6(–9) μ, germinating by globose conidia.

TYPE LOCALITY: Baton Rouge, Louisiana.

HABITAT: Angiosperm wood.

ILLUSTRATIONS: Lowy, Bull. Torrey Bot. Club **81**: 301. *f. 1–11.*

Specimen examined: Louisiana, *B. Lowy 8251,* TYPE, LSU.

One part of the type collection proved to be sterile and was covered with peculiar clavate structures in place of basidia. These were very thick-walled with the walls unevenly thickened from inward gelatinization, and possessed clamp-connections. Sometimes the stainable lumen appeared to project beyond the end of the sterile structure because the wall was of normal, narrow width at the apex. Type material with basidia, and basidiospores also showed these structures amongst the basidia, although in smaller numbers. It cannot be judged from one collection whether the presence of these structures is a specific character and therefore I have not included it in the description.

3. DACRYMYCES ENATUS (Berk. & Curt.) Massee, Jour. Myc. **6**: 182. 1891, var. **enatus.**

Tremella enata Berk. & Curt. Grevillea **2**: 20. 1873.

?*Dacrymyces castaneus* Rabenh. Krypt.-Flor. **1**: 53. 1844.

?*Dacrymyces fuscominus* Coker, Jour. Elisha Mitchell Soc. **35**: 171. 1920.

Arrhytidia enata (Berk. & Curt.) Coker, Jour. Elisha Mitchell Soc. **43**: 237. 1928.

Dacrymyces deliquescens var. *castaneus* Bourd. Bull. Soc. Myc. France **48**: 206. 1932.

Dacrymyces gangliformis Brasf. Lloydia **3**: 105. 1940.

Basidiocarp dark chestnut brown sometimes with a purple tint, or yellowish-brown, drying very dark brown to dull black, arising as convoluted pustules attached by a broad, central point, often with effused margins which frequently coalesce to form a large irregular mass, this aggregation always retaining evidence of pustular origin, single basidiocarps 1–2 mm in diameter, forming masses up to 4 cm in extent; tough-gelatinous to rubbery, drying horny; hyphae smooth, thin-walled, sometimes with strongly gelatinized walls, with numerous, conspicuous clamp-connections; probasidia with basal clamp-connection, (15–)17–32(–45) × 3(–5)μ; dikaryophyses with basal clamp-connections and irregularly branched apices projecting beyond the basidia present with varying frequency; basidiospores curved-cylindrical, tardily 1-septate, 8–13 × 3–4.5 μ, germinating by germ tubes.

TYPE LOCALITY: Lower Carolina.

HABITAT: Angiosperm or gymnosperm wood.

ILLUSTRATIONS: Coker, Jour. Elisha Mitchell Soc. **43**: *pl. 48, f. 1, 2;* Brasfield, Lloydia **3**: 159, *f. 6–10.*

Specimens examined: Brazil (1); England (1); U.S.A.: California (1), Iowa (2), Massachusetts (4 including the TYPE of *D. gangliformis, Linder and Whelden 142,* FH; IA), New York (1), North Carolina (2 including the TYPE of *Arrhytidia enata, Coker 4989,* NCU; IA and the TYPE of *D. fuscominus, Couch 4075,* FH; IA), Ohio (1).

I have adopted Coker's conception of *Dacrymyces enatus,* since his description under the name *Arrhytidia enata* Coker contains the detail necessary for positive identification of collections as this species.

It seems likely that *Dacrymyces fuscominus* Coker is the same as *Dacrymyces enatus* var. *enatus,* for the basidiocarps are similar in form, color and consistency, the hyphae are thin-walled with numerous clamp-connections in both species, and the basidiospores are tardily 1–3-septate with the same size range. In spite of these similarities, I have a certain reservation about equating these two species, for I have not had the opportunity to observe the dark, greenish-olive color of the fresh basidiocarps mentioned by Brasfield (**1938**) and Lowy (**1956**) in connection with *Dacrymyces fuscominus.* The collections I have studied

were herbarium specimens and neither those of *Dacrymyces fuscominus* nor those of *Dacrymyces enatus* showed any greenish color.

The species may be recognized by the color and consistency of the basidiocarp, the conspicuous clamp-connections on the hyphae, and the dikaryophyses with irregularly branched tips. The color of the basidiocarp is not lost on prolonged soaking, which is unusual. The variety *enatus* is characterized by basidiospores which are tardily 1-septate, possess narrow walls and septa and measure 8–13 × 3–4 μ.

4. DACRYMYCES ENATUS var. **macrospora** var. nov.

A specie typica recedit sporis mox triseptatis; septis parietibusque crassis et gelatinosis.

Basidiocarps 3–4 mm in diameter, forming masses many centimeters in extent by coalescence; probasidia 35–40(–49) × 3 μ; basidiospores plump-allantoid, hyaline or brownish, early and distinctly 3-septate, the septa and spore walls becoming wide and gelatinous, 13–15 × 5–7 μ.

TYPE LOCALITY: Barro Colorado Island, Panama.

HABITAT: Angiosperm wood.

Specimens examined: Panama (2 including *G. W. Martin and A. L. Welden 8662*, TYPE, IA; ALTA).

In the type collection the hyphae and basidiospores are pale brown under the lens instead of hyaline, the usual condition. This pigment is not present in the second collection, which agrees in other particulars. This variety is distinguished on the basis of the early 3-septate, larger basidiospores with wide gelatinous walls and septa.

5. DACRYMYCES ABIETINUS Schroet. Krypt.-Fl. Schles. **3**(1): 400. 1888, var. **abietinus.**

?*Dacrymyces azaleae* Schw. Trans. Am. Phil. Soc. II. **4**: 186. 1832.

Dacrymyces stillatus Fries, Hymen. Eur. 699. 1874 (not *Dacrymyces stillatus* Fries, Syst. Myc. **2**: 230. 1822; not *Dacrymyces stillatus* Tul. Ann. Sci. Nat. Bot. III. **19**: 219. 1853).

?*Dacrymyces San-Angustinii* Kob. Sci. Rep. Tokyo Bunr. Daig. B **4**: 122. 1939.

Basidiocarp pale orange to brown, drying amber to very dark brown, turbinate or flattened-pustulate with a slightly depressed center, lacking convolutions, when on decorticate wood attached by a point or a short stalk, when on corticate wood attached by a radicating stalk which goes through the bark and enters the wood below, single basidiocarps 1–5 mm in diameter, up to 14 mm by fusion (on corticate wood only);

gelatinous; hyphae smooth, thin-walled, sometimes becoming strongly, irregularly gelatinized in old basidiocarps, usually with conspicuous clamp-connections; probasidia (43–)45–77 × 4–7 μ with basal clamp-connections frequently accompanied by dikaryophyses with clamp-connections which project beyond the basidia; basidiospores deep orange in mass (Martin), curved-cylindrical to plump-allantoid, 3–7-septate (finally 7–9-septate), septa distinct, occasionally becoming widened, (10.2)14–25 × 6–9 μ, germination by germ tube or ovoid conidia.

TYPE LOCALITY: Germany.

HABITAT: Gymnosperm wood and rarely on angiosperm wood.

ILLUSTRATIONS: Berkeley, Outline Brit. Fung. *pl. 18, f. 8;* Brefeld Unters. **7**, *pl. 10, f. 9–11;* Coker, Jour. Elisha Mitchell Soc. **35**: *pl. 23, f. 12; pl. 63, f. 3, 4;* Brasfield, Am. Midl. Nat. **20**: 271. *f. 29–32.*

Specimens examined: Canada: Ontario (2); Sweden (1); U.S.A.: Alabama (1), California (4), Iowa (1), Louisiana (1), Maine (1), Massachusetts (1), New York (1).

The spores are very slowly septate and they may germinate by conidia, or more commonly by germ tube, from the 3-septate stage onward. There is an unusual range of size in the spores of *Dacrymyces abietinus* as they range from 10.2 to 25 μ in length. Since this range was found not only amongst different collections but in a single collection, it would appear that for this species such a range in size must be accepted.

6. DACRYMYCES ABIETINUS var. TRISEPTATUS Olive, Mycologia **40**: 598. 1948.

Basidiocarps orange-yellow, drying amber, pustulate, frequently convoluted, attached by a short stalk or radicating base; hyphae septate (often with collapsed clamp-connections or bulbous septa); basidiospores 1–3–7-septate but predominantly, and sometimes entirely, 3-septate, 12–22 × 6–8 μ.

TYPE LOCALITY: Louisiana.

HABITAT: Gymnosperm wood and rarely on angiosperm wood.

ILLUSTRATIONS: Olive, Mycologia **40**: 600. *f. 3, 19–20.*

Specimens examined: Australia (1); U.S.A.: Iowa (2), Louisiana (1) (*Olive 70*, LSU, TYPE of variety *triseptatus*), Wisconsin (1).

All the features of this variety have been found associated with the large 7-septate spores characteristic of *Dacrymyces abietinus* and the original description notes the presence of typical basidiospores associated with the smaller 3-septate ones. In the course of this work three collections were encountered which agreed well with Olive's description. In one the great majority of spores were 3-septate and small for the

species; in the other two collections all the spores were small and 3-septate. It was apparent that collections of this kind would be practically impossible to identify. They would probably be thought to be *Dacrymyces deliquescens*, for the spores of this species are also 3-septate and fall within the range of size shown by *Dacrymyces abietinus* var. *triseptatus*. Therefore, the recognition of this variety seems justified although its features could be included easily in the species description. It appears not rare since out of twelve collections of *Dacrymyes abietinus* studied three could be determined as this variety. *Dacrymyces abietinus* var. *triseptatus* can be distinguished from *Dacrymyces deliquescens* by the plump-allantoid spores which are nearly oval in some cases and often only twice as long as wide. In addition, a careful search will often reveal some spores well outside the range of spore length, 10–16.5 μ, characteristic of *Dacrymyces deliquescens*.

The original description of *Dacrymyces azaleae* Schw. is inconclusive and Coker (**1920**) reports the type material sterile. In the Morgan collection deposited at the State University of Iowa (IA) there is a collection from Alabama, *Atkinson 1643*, labelled *Dacrymyces azaleae*. There is no serious discrepancy between the appearance of these basidiocarps, or the substrate, which is angiosperm wood, and Schweinitz's description supplemented by Coker's notes. Careful study showed that this collection agrees in every respect with *Dacrymyces abietinus* var. *abietinus* as described above. If *Dacrymyces azaleae* is interpreted on the basis of this Alabama collection then it is synonymous with *Dacrymyces abietinus* var. *abietinus*. If *Dacrymyces azaleae* is the same as *Dacrymyces abietinus* then it is the earlier valid name and should be adopted. It would be inadvisable, however, to replace a well known and clearly defined name with one so poorly defined and little known until additional collections are available.

Martin (**1952**) considered the valid name for *Dacrymyces abietinus* to be *Dacrymyces stillatus* Fries 1822. In Kennedy (**1956a**) reasons are advanced for considering *Dacrymyces stillatus* a *nomen ambiguum* and *Dacrymyces abietinus* Schroet the correct name. In that paper *Tremella abietina* Pers. and *Tremella lacrymalis* Pers. should have been cited as the species associated with *Dacrymyces deliquescens*.

7. DACRYMYCES PUNCTIFORMIS Neuh. Arkiv för Bot. **28A**[1]: 40. 1936.
Dacrymyces tortus Fries, Elench. Fung. **2**: 38. 1828 (teste Neuhoff).
?*Dacrymyces pallidus* Coker, Jour. Elisha Mitchell Soc. **35**: 171. 1920.

?*Dacrymyces hyalinus* Overholts, Bull. Torrey Bot. Club **49**: 166. 1922 (as *hyalina*).

?*Dacrymyces caesius* Lloyd, Myc. Writ. **7**: 1348. 1925.

Dacrymyces deliquescens f. *nigricans* Bourd. & Galz. Hymén. de France 67. 1928, pro parte.

Dacrymyces deliquescens f. *myriadeus* Bourd. & Galz. Hymén. de France 68. 1928, pro parte.

Dacrymyces romellii Neuh. Arkiv för Bot. **28A**[1]: 42. 1936.

Basidiocarp amber color or sordid yellow (sometimes with a greenish tinge), drying amber to brown, not collapsing on drying and visible as amber droplets or 'raisins,' pustulate, flattened and commonly centrally depressed, occasionally with convolutions, attached by a central point (rarely substipitate), 0.5–2 mm in diameter; firm-gelatinous; hyphae smooth or rough, thin-walled (sometimes there is a mixture of thin-walled hyphae and hyphae with irregularly thickened, gelatinous walls), all with numerous, conspicuous clamp-connections; probasidia (20–)27–45 × 3–4 μ with basal clamp-connections, accompanied by dikaryophyses, with clamp-connections, extending beyond the basidia (rarely lacking in some of the more luxuriant forms); basidiospores cylindrical, slightly curved, predominantly aseptate, very tardily 1–3-septate with narrow septa, (7–)10–15 × 3–5 μ, germinating by germ tube.

TYPE LOCALITY: Europe.

HABITAT: Gymnosperm wood.

ILLUSTRATIONS: Neuhoff, Arkiv för Bot. **28A**[1]: 41. *f. 1, d, g; pl. 4, B; pl. 7;* Brasfield, Am. Midl. Nat. **20**: 229. *f. 15–17;* Kobayasi, Sci. Rep. Tokyo Bunr. Daig. B. **4**: 115. *f. 3, C; pl. 9, f. A.*

Specimens examined: Canada: Nova Scotia (2), Ontario (4); Sweden (5); U.S.A.: California (1), Iowa (2), Louisiana (1), Massachusetts (1), New Mexico (2), New York (1), Oregon (3).

Dacrymyces punctiformis may be recognized by the pattern formed by its outstanding features of conspicuous clamp-connections on the hyphae, dikaryophyses with clamp-connections and the narrow, slightly curved, very tardily septate basidiospores.

This species may be parasitized by *Tremella obscura* Christensen.

Dikaryophyses with clamp-connections were found to be an important diagnostic feature. However, the fact that Neuhoff (**1936**), Kobayasi (**1939**) and Olive (**1946**) make no mention of them leads one to conclude they are absent from some collections. Possibly their development is modified by the environment or else there is a phase without them. The number of sterile elements in the hymenium in this and other species varies from collection to collection or even from one

basidiocarp to another in the same collection. Sometimes they are so numerous they alternate with the basidia or even out-number them; at other times they occur very sparingly. It seems probable that the production of sterile hymenial elements in these fungi is related to the nutrition of the fungus, and that better growth conditions lead to the development of more basidia. In spite of this variability a search for dikaryophyses will nearly always reveal them in the basidiocarps of this species.

According to Neuhoff (**1936**) and Nannfeldt (private communication) *Dacrymyces tortus* Fries 1828 is synonymous with *Dacrymyces punctiformis*. Since Neuhoff did not reinstate the name, and since *Dacrymyces tortus* has been applied to several different species and never adequately defined by any author, I prefer to retain the name *Dacrymyces punctiformis* for the present.

On the basis of part of a collection determined by Coker, and his notes with his original collections made available through the courtesy of Dr. B. Lowy, I have assigned *Dacrymyces pallidus* Coker to a provisional position as a synonym of *Dacrymyces punctiformis*. It seems inadvisable to decide finally on its position until more collections become available.

8. DACRYMYCES FALCATUS Brasf. Lloydia **1**: 154. 1938.

Basidiocarp pale orange to dull yellow, drying reddish-brown, inconspicuous, flattened-pustulate to somewhat patellate, smooth or convoluted, attached by a central point, 0.5–3 mm in diameter; gelatinous, drying horny; hyphae smooth, thin-walled, septate; probasidia with basal septa and abruptly obtuse bases, 40–60(–70) × 6–8 μ; basidiospores allantoid, very strongly curved, distinctly and early septate; multiseptate, finally with 15 or more septa, strongly apiculate, (20–)23–27(–29) × 6–8 μ.

TYPE LOCALITY: Prov. Chiriqui, Panama. Also known from Jamaica, B.W.I.

HABITAT: Angiosperm wood.

ILLUSTRATION: Brasfield, Lloydia **1**: 159. *f. 7–11.*

Specimens examined. Panama (2 including *G. W. Martin 2344*, TYPE, IA and *G. W. Martin 2109*, paratype, IA).

This species differs from known species of *Dacrymyces* in the very strongly curved (grub-like) spores with a large, indefinite number of distinct septa. The abruptly obtuse base of the basidium is also unusual.

In describing this species Brasfield speaks of globoid, septal swellings on the hyphae. Since I have seen similar swellings in collections

of *Dacrymyces deliquescens* both from this area and the United States, I did not refer to them in the species description. The swellings appear due to local gelatinization of the wall and are quite common in these collections of *Dacrymyces falcatus*.

9. DACRYMYCES PALMATUS (Schw.) Bres. in Hoehn. Oesterr. Bot. Zeit. **54**: 425. 1904.

?*Naematelia rubiformis* Fries, Syst. Myc. **2**: 228. 1822.
Tremella palmata Schw. Trans. Am. Phil. Soc. II. **4**: 186. 1832.
Dacrymyces chrysospermus Berk. & Curt. **2**: 20. 1873 (as *chrysosperma*).
Dacrymyces tremelloides Karst. Bidr. Finl. Nat. Folk **37**: 241. 1882.
Dacrymyces aurantius sensu Farl. Appalachia **3**: 248. 1883 (not *Tremella aurantia* Schw. Schr. Nat. Ges. Leipzig **1**: 114. 1822).
Dacrymyces multiseptatus Beck, Fl. Hernstein 126. 1886.
Guepiniopsis aurantius (Schw.) Pat. Jour. de Bot. **7**: 344. 1893.
Dacrymyces flabellus Ell. & Ev. Proc. Acad. Nat. Sci. Phila. **46**: 324. 1894 (as *flabella*).
?*Dacrymyces digressus* Lloyd, Myc. Writ. **5**: 620. 1916.
?*Dacryomitra depallens* Lloyd, Myc. Writ. **5**: 803. 1918.
Dacryopsis palmata (Schw.) Lloyd, Myc. Writ. **6**: 989. 1921.
Dacryomyces palmatus (Schw.) Burt, Ann. Mo. Bot. Gard. **8**: 361. 1921.
Dacryomitra ramosa Wehmeyer, Papers Mich. Acad. Sci. **20**: 249. 1935.
?*Dacrymyces rubiformis* (Fries) Neuh. Arkiv för Bot. **28A**[1]: 51. 1936.

Basidiocarp bright orange, drying orange-red, conspicuous when dry, sessile, pulvinate or flabellate, or stipitate, with a spathulate, or convoluted, patellate or cupulate head up to 7 mm wide, 5 mm high, attached by a white radicating base, commonly erumpent in clusters to form an erect, petaloid, cerebriform or stalked and pileate compound sporocarp from 3 to 6 cm in longest dimension; gelatinous, collapsing when old; stalk and rooting base with a white cortex composed of cylindrical or clavate, septate hyphae with thick, gelatinized walls, often rough on the surface, up to 80 μ in length and 7 μ wide (these apparently lacking in a few collections or becoming so gelatinized as to take no stain); internal hyphae thin-walled, smooth or rough, septate, occasionally with bulbous septa; probasidia (45–)50–70(–80) × 3–6 μ with basal septa; basidiospores orange in mass, curved-cylindrical, distinctly and early 7-septate, 17–21(–25) × 6–8 μ, germinating by oval conidia or germ tubes.

TYPE LOCALITY: Bethlehem, Pennsylvania.

HABITAT: Gymnosperm and less commonly angiosperm wood.

ILLUSTRATIONS: Coker, Jour. Elisha Mitchell Soc. **35**: *pl. 23, f. 10; pl. 63, f. 6–7;* Farlow, Icon. Farl. *pl. 100;* Bresadola, Icon. Myc. **23**: *pl. 1126, f. 2;* Wehmeyer, Papers Mich. Acad. Sci. **20**: *f. 3;* Brasfield, Am. Midl. Nat. **20**: 231. *f. 42–45;* Kobayasi, Sci. Rep. Tokyo Bunr. Daig. B **4**: *pl. 11, f. B;* Kennedy, Mycologia **48**: 313–315. *f. 1–3.*

Specimens examined: Brazil (1); Canada: Alberta (1), Nova Scotia (2), Ontario (15), Quebec (1); U.S.A.: California (3), Idaho (3), Indiana (3), Iowa (1), Louisiana (11), Maine (3), Maryland (1), Michigan (2), Minnesota (3), Montana (1), New Hampshire (4), New York (5), North Carolina (3), Oregon (3), Tennessee (3), Vermont (1), Virginia (1), Washington (2).

The characteristics of this species have been discussed in detail in a previous paper (Kennedy, **1956**). It may be said here that *Dacrymyces palmatus* shows the greatest variation in basidiocarp form of any member of the genus. However, the basidiocarps are always a striking, bright orange color when moist and orange-red when dry. They are composed of thin-walled, septate hyphae and bear a varying number of clavate, cortical hairs with thick gelatinous walls on the stalk and radicating base. In addition, the spores are large and rapidly become 7-septate.

10. DACRYMYCES DELIQUESCENS var. **minor** (Peck) var. nov.

Dacrymyces deliquescens f. *lutescens* Fries, Syst. Myc. **2**: 230. 1822 (teste Neuhoff).

Dacrymyces minor Peck, Ann. Rep. N. Y. State Mus. **30**: 49. 1877.

Dacrymyces deliquescens (Bull.) Duby sensu Burt, Ann. Mo. Bot. Gard. **8**: 382. 1921.

Dacrymyces subochraceus sensu Burt, Ann. Missouri Bot. Gard. **8**: 384. 1921 (not *Tremella subochracea* Peck, N. Y. State Mus. Report **34**: 43. 1881).

Dacrymyces deliquescens f. *fagicola* Bourd. & Galz. Hymén. France 67. 1928.

Dacrymyces lutescens Bref. sensu Neuhoff, Arkiv för Bot. **28A**[1]: 41. 1936.

Basidiocarp sordid orange or yellow, often with an olivaceous tinge when young, drying amber and very inconspicuous, pulvinate, smooth and centrally depressed or slightly convoluted, rarely cerebriform, 0.5–3 mm in diameter, commonly discrete, sometimes in crowded groups but scarcely truly coalescing, attached by a central point or a very short stipe; firm-gelatinous; hyphae smooth, rarely roughened, thin-walled,

septate; probasidia (22–)25–36(–46) × 3–4 μ with basal septa, sometimes accompanied by simple, septate dikaryophyses; basidiospores yellow in mass, curved-cylindrical, finally distinctly 3-septate, 8–15 × 3–4(–6) μ, germinating by spherical conidia or germ tubes from 1-, 2- or 3-septate spores.

TYPE LOCALITY: Buffalo, New York.

HABITAT: Angiosperm or rarely gymnosperm wood.

ILLUSTRATIONS: Coker, Jour. Elisha Mitchell Soc. **35**: *pl. 64, f. 1–2;* Neuhoff, Arkiv för Bot. **28A**[1]: 41. *f. 1, i,* Brasfield, Am. Midl. Nat. **20**: 229. *f. 18–22;* Kobayasi, Sci. Rep. Tokyo Bunr. Daig. B **4**: 115. *f. 3 B; pl. XI, f. G.*

Specimens examined: Brazil (1); Canada: Nova Scotia (1), Ontario (4); England (4); Germany (1); Sweden (3); U.S.A.: California (2), Illinois (3), Indiana (3), Iowa (21), Maine (1), Massachusetts (4), New York (2 including the LECTOTYPE, *G. W. Clinton 44,* NYS), Washington (1), Wisconsin (1).

This variety can be recognized by the very small, usually greenish-yellow pustules which show very little coalescence, even when crowded, and which are practically invisible when dry. The spores are slowly 3-septate with indistinct septa and narrow walls. Usually both probasidia and spores appear smaller than in other varieties of this species.

Dacrymyces deliquescens var. *minor* is often parasitized by *Tremella obscura* Christensen, *Platygloea peniophorae* Bourd. & Galz. and *Platygloea arrhytidiae* Olive. Two of these species produce hyphae with clamp-connections which may be confused with the host hyphae. None of these species forms basidiocarps on the *Dacrymyces* host; instead, the basidia grow intermixed with the host basidia. In the case of a *Platygloea* parasitic on *Dacrymyces* it appears as if septate dikaryophyses are present if the basidia of the parasite are immature. It was interesting to find that collections determined as *Dacrymyces lutescens* Bref. sensu Neuhoff were also parasitized by a *Tremella* and a *Platygloea.*

Examination of the type collection of *Dacrymyces minor* Peck revealed a packet containing two distinct collections. One of these, *G. W. Clinton 44,* Buffalo, New York, was homogeneous and agreed with Peck's description in all essential points. It was designated the lectotype. The second collection, *C. H. Peck,* Sand Lake, New York, contained a mixture of *Dacrymyces minor* and *Dacrymyces abietinus.* The basidiocarps of the designated type collection were very small, discrete pustules less than a millimeter in diameter and of a pale, drab-orange color when moistened. They were attached by a point to angiosperm wood. The probasidia measured 27–31(–36) × 3 μ. The basidiospores were curved-cylindrical with 3 indistinct septa and measured 10–13(–15)

× 3–4.5 μ. Some of the basidiocarps were parasitized by *Tremella obscura*. The *Dacrymyces minor* material of the second collection possessed the same characteristics as the type material except that the basidiocarps did have the faint greenish color mentioned in the original description. This color often disappears when the basidiocarps become older. Both these collections were cited with the original description.

11. DACRYMYCES DELIQUESCENS (Mérat) Duby, Bot. Gall. **2**: 729. 1830. var. **deliquescens.**

[*Tremella deliquescens* Bull. Hist. Champ. France 219. 1791.]

[*Dacryomyces stillatus* Nees, Syst. Pilze Schw. 89. 1816 stat. imp.]

Tremella deliquescens Bull. ex Mérat, Nouv. Fl. Env. Paris 2 ed. **1**: 28. 1821.

Gyraria lachrymalis S. F. Gray, Brit. Plants **1**: 595. 1821.

Dacrymyces stillatus Fries, Syst. Myc. **2**: 230. 1822. stat. imp.

Calloria stillata Fries, Summa Veg. Scand. 359. 1849. stat. imp.

Dacrymyces lacrimalis Bon. Handb. Myk. 149. 1851.

Dacrymyces lutescens Bref. Unters. **7**: 152. 1888.

Hormomyces abietinus Karst. Hedwigia **29**: 271. 1890.

Dacrymyces deliquescens (Bull.) Duby sensu Bourd. & Galz. Hymén. France 67. 1928.

Dacrymyces deliquescens (Bull.) Duby sensu Neuhoff, Arkiv för Bot. **28A**[1]: 40. 1936.

Basidiocarp bright orange-yellow to brownish-orange, drying dark orange to reddish-brown, pustulate and slightly folded to cerebriform, or flattened-discoid and lacking convolutions, 1–5 mm in diameter, sometimes coalescing to form masses up to 15 mm in extent, commonly attached by a point, sometimes by a short stalk and slightly rooted; firm-gelatinous; hyphae smooth, rarely roughened, thin-walled, septate; probasidia (22–)24–50(–55) × 3–4.5 μ, with basal septa; basidiospores deep orange in mass, occasionally ochraceous, curved-cylindrical, early and distinctly 3-septate, the walls and septa finally wide and gelatinous, (9–)11–16 × 3–6 μ, germinating by germ tubes or globose conidia. The basidiocarps frequently contain arthrospores (often called oidia) which are catenulate, 1- or 2-celled, mostly 8–16 × 3.5–6 μ. The arthrospores may occur in separate sporocarps which are reddish-orange or yellow and very soft-gelatinous in consistency.

TYPE LOCALITY: Europe.

HABITAT: Gymnosperm or less commonly angiosperm wood.

ILLUSTRATIONS: Bulliard, Herb. France *pl. 455, f. 3;* Tulasne, Ann. Sci. Nat. Bot. III **19**: *pl. 12, f. 13–19*; *pl. 13, f. 1–18*; Brefeld, Unters. **7**: *pl. 9;* Dangeard, Le Botaniste **4**: 136. *pl. 6;* Buller, Res. on Fungi

2: 173. *f. 59;* 175, *f. 60;* Farlow, Icon. Farl. *pl. 100;* Neuhoff, Arkiv för Bot. **28A**[1]: 41. *f. 1, h;* Brasfield, Am. Midl. Nat. **20**: 231. *f. 23–28;* Kobayasi, Sci. Rep. Tokyo Bunr. Daig. B **4**: *f. 3, A; pl. XI, f. F.*

Specimens examined: Brazil (3); Canada: Nova Scotia (4), Ontario (1); England (5); Greece (2); Latvia (1); the Netherlands (2); Panama (3); Sweden (2); U.S.A.: California (3), Iowa (20), Louisiana (1), Maine (3), Massachusetts (5), North Carolina (1), Ohio (1), Vermont (1).

This variety may be recognized by the distinctly and early 3-septate basidiospores which finally develop wide walls and septa. Arthrospores are nearly always present, either in separate sporocarps or in the basidiocarps, but the sporocarps do not occur frequently enough to be used as a key character, as has been done by Neuhoff (**1936**), and Kobayasi (**1939**).

Although the basidiospores are usually curved-cylindrical there is more variation in shape than is generally realized. Sometimes the spores are oval to almost globose, sometimes subpyriform and strongly attenuated at the apiculus end. However, these spores of unusual shape are generally accompanied by at least a few spores of the typical shape.

The somewhat puzzling variation in the author citations of the well-known name *Dacrymyces deliquescens* might be explained here. The name is correctly given as *Dacrymyces deliquescens* (Mérat) Duby although neither of these men contributed much to an understanding of the species. In 1829 Duby described *Dacrymyces deliquescens* based on *Tremella deliquescens* Bull., which he gave as a synonym. He was thus first to make this combination and the name has frequently been written *Dacrymyces deliquescens* (Bull.) Duby. However, in 1821 Mérat lists *Tremella deliquescens* Bull. with a short description of the perfect stage. This description is much inferior to that of Bulliard but the date of publication makes the citation of Mérat's name necessary.

12. DACRYMYCES DELIQUESCENS var. **ellisii** (Coker) var. nov.

?Dacrymyces cerebriformis Bref. Unters. **7**: 153. 1888.

Dacrymyces ellisii Coker, Jour. Elisha Mitchell Soc. **35**: 167. 1920.

Dacrymyces harperi Bres. Ann. Mycol. **18**: 53. 1920.

Dacrymyces cerebriformis Bres. sensu Lloyd, Myc. Writ. **7**: 1197. 1923.

Dacrymyces cerebriformis Bref. sensu Neuhoff, Arkiv för Bot. **28A**[1]: 43. 1936.

Basidiocarp bright orange-yellow to brown-orange becoming brown when old, conspicuous when dry, pustulate, becoming convoluted, frequently coalesced to form erumpent or raised, cerebriform clusters up

to 2 cm in extent, when on corticate wood attached by a tough, pallid, stalk-like, rooting base which is visible when the bark is removed, and which passes through the bark to penetrate the wood; where coalescence occurs there is a common radicating base, when on decorticate wood the rooting stalk is shorter and the basidiocarps appear substipitate; firm to tough-gelatinous but becoming soft when old and finally collapsing; internal hyphae thin-walled, usually rough, or at least some rough hyphae present (occasionally completely smooth), septate, hyphae of rooting stalk with thin walls and irregularly thickened, gelatinous walls; probasidia (27–)34–52(–62) × 3–5 μ with basal septa, sometimes accompanied by simple, septate dikaryophyses; basidiospores deep orange in mass, curved-cylindrical, strongly apiculate, becoming 3-septate with distinct or indistinct septa, 10–17 × 3–7 μ, germinating by germ tubes (usually) or by oval conidia.

TYPE LOCALITY: North Carolina.

HABITAT: Angiosperm and very rarely gymnosperm wood.

ILLUSTRATIONS: Coker, Jour. Elisha Mitchell Soc. **35**: *pl. 23, f. 11; pl. 50, f. 4; pl. 63, f. 8;* Brasfield, Am. Midl. Nat. **20**: 231. *f. 36–41;* Martin, Univ. Iowa Stud. Nat. Hist. **19**(3): 106. *pl. 1, f. 8.*

Specimens examined: Canada: Ontario (2); Germany (1); Panama (2); U.S.A.: Indiana (3), Iowa (23), Maine (1), Massachusetts (1), Michigan (2), Missouri (1), Nebraska (1), New Hampshire (3), New Jersey (1), New York (7), North Carolina (1), Ohio (1), Vermont (1).

This variety can be distinguished by the presence of the tough-gelatinous radicating base or substipe, the tendency to form clusters of basidiocarps, the usually rough hyphae, and the basidiospores with narrow septa and walls and a marked apiculus.

In connection with this variety Brasfield reported that the basidiospores form conidia up to 5 × 3 μ. In this study conidia larger than 3 μ have not been seen and the majority measured 1–2 μ in diameter. Since complete disarticulation of spore segments, which measure 4–5 μ, has been observed in collections of this variety and in other *Dacrymyces* species, it is suggested that these segments, which round up after separation, have sometimes been considered conidia.

It has been a difficult problem to decide how to deal with the three species *Dacrymyces deliquescens, Dacrymyces minor* and *Dacrymyces ellisii.* They are obviously closely related and appear to be like the three points of a triangle joined to one another by characteristics in common and intermediate forms. This situation has been described by Olive (**1947**), whose remarks suggested to me that there might be only one species involved here. So far as I have been able to determine, and herbarium material is abundant, there is no pattern of characteristics

which can be described that holds true for any of these species all the time or even most of the time. No statement can be made about any characteristic that does not require qualification. Not only are the specific boundaries indistinct, but a number of collections have been found that are exactly intermediate in character between all three combinations of these species. Such collections can be determined only in an arbitrary manner, regardless of experience.

It is suggested that there is here only one polymorphic species with a number of intergrading phases. One would be justified in deciding that all these collections should be classified as *Dacrymyces deliquescens*, the earliest valid name of the three specific names involved, for there is no consistent way to draw specific lines between these three species. However, many workers have been able to identify collections as one of these three species, for there are many so-called typical collections of them. Furthermore, a single description would be so long, and the features would require so much qualification, that it would be unusually difficult to comprehend the species. Therefore, it is considered that the species *Dacrymyces deliquescens* can be presented most clearly as composed of the three varieties: variety *deliquescens*, variety *minor* and variety *ellisii* corresponding to the three species with these specific epithets.

DOUBTFUL AND EXCLUDED SPECIES

Dacrymyces chrysocomus Tul. Ann. Sci. Nat. III **19**: 211. 1853.

This species was transferred to the genus *Guepiniopsis* by Brasfield (**1938**). It has been so classified in these studies.

Dacryomyces concavus Lloyd, Myc. Writ. **7**: 1162. 1922, is a *nomen nudum*.

Dacrymyces conglobatus Peck, Ann. Rep. N. Y. State Mus. **32**: 37. 1880.

According to Martin (**1952**), this species belongs in the genus *Ditangium*. Examination of the type collection shows it to be *Ditangium cerasi* (Tul.) Const. & Duf.

Dacrymyces conigenus Niessel, in Rab.-Winter, Fungi Eur. No. 2628. 1881.

This collection yielded no basidia of any kind, but there were numerous, tiny, round spores. According to Höhnel (**1908**), this species is *Pseudopatellina conigena* (Niessl) Höhn. It is clearly not a *Dacrymyces*.

Dacryomyces cupularis Lloyd, Myc. Writ. **7**: 1225. 1923.

Lloyd's description reads as follows: "Sessile, 3–4 mm in diameter, concave, cup shape. Color pale yellow with a slight greenish tint. Basidia forked. Spores not found." The specimen was from Tasmania.

Brasfield (**1940**) assigned three collections from Tasmania to this species. These three collections were examined again and found to be *Ditiola radicata* Fries. Possibly this was the species Lloyd had but I have not seen his collection. However, *Dacrymyces cupularis* Lloyd sensu Brasfield belongs in the genus *Ditiola*.

Dacryomyces flavus Lloyd, Myc. Writ. **7**: 1345. 1925, is a *nomen nudum*.

Dacrymyces fragiformis Fries, Syst. Myc. **2**: 229. 1822.

The description reads as follows, "Subcompactus, rotundus, ruber, plicis confertis sublobatis. Exsiccatus 4–6 lin. latus, ceterum ad unciam magnus, colore fragi, intus pallescens. Ex lobis quasi constat haec species." Although I have seen no type material there are a number of collections in the IA herbarium identified as this species. They are all *Hormomyces aurantiacus* Bon. Furthermore, the literature descriptions of this species suggest a *Hormomyces*. It appears justifiable to exclude this species from the genus.

Dacrymyces pellucidus Schw. Trans. Am. Phil. Soc. II **4**: 186. 1832.

According to Martin (**1952**), this species is identical with *Tremella concrescens* (Fries) Burt.

Dacrymyces radicatus (Fries) Donk, Med. Nederl. Mycol. Ver. **18–20**: 120. 1931.

Donk transferred *Ditiola radicata* Fries to the genus *Dacrymyces* and in this he was followed by Neuhoff (**1936**). I consider the genus *Ditiola* distinct and therefore I would exclude this species from the genus *Dacrymyces*.

Dacrymyces stipitatus (Bourd. & Galz.) Neuhoff, Arkiv för Bot. **28A**[1]: 42, 1936.

A collection of this species determined by Neuhoff is *Ditiola radicata* Fries.

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A NEW GENUS IN THE PROTOMYCETACEAE

C. L. KRAMER [1]

(WITH 17 FIGURES)

Taphrina osmundae, as described by Nishida (**1911**), produces large, yellow to brown, somewhat swollen, effused spots on the leaves of *Osmunda regalis* L. var. *japonica* Willd. The asci were described as oblong or oblong-clavate, 32–44 $\mu \times$ 17–25 μ, without stalk cells, and the ascospores as minute and numerous in the asci.

Mix (**1947**) adds several significant features to the description of *Taphrina osmundae*. He describes the mycelium as growing within locules in the outer epidermal wall, appearing in the earliest stages as septate hyphae of short segments, and according to his interpretation unspecialized hyphal branches (haustoria) were seen (in some cases) to extend into the cell-cavity beneath. As this mycelium matures, large intercallary swellings form in the mycelium, which Mix refers to as ascogenous cells. The ascus arises as a papilla from one of these ascogenous cells, and according to Mix emerges by rupture of the outer wall of the locule. As the papilla enlarges, a septum forms across the basal portion of it, so that at maturity each ascus is provided with an empty stalk cell. The stalk cell, according to Mix, was somewhat triangular in outline except at its base where a foot-like expansion remained within the locule.

Spore formation in *Taphrina osmundae*, as described by Mix (l.c.), usually begins before ascus emergence. The formation of these spores, which he refers to as conidia, occurs in a peripheral layer of protoplasm, leaving a large vacuole in the center of the cell. The mature ascus, as Mix described it, contains a large number of conidia, closely packed in a peripheral layer.

A fungus very similar to *Taphrina osmundae*, which causes necrotic lesions on the fronds of *Osmunda cinnamomea* L., was first collected by B. B. Higgins, May 26, 1938, at Hamilton, Georgia. Mix (**1947**) described it as a new species, *T. higginsii*. The author collected this spe-

[1] A portion of a thesis presented to the Graduate School of Kansas University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. I wish to express my sincere appreciation to the late Dr. A. J. Mix and to Dr. N. M. McClung for their interest and encouragement during the course of this study.

cies in abundance at the same location seventeen years later. Although the fern *Osmunda cinnamomea* occurs throughout the eastern half of the United States, this fungus has been collected only in Georgia and Michigan.

The morphology of *Taphrina higginsii*, as described by Mix (l.c.), is very similar to that of *T. osmundae*. The habit of the mycelium, development of the ascogenous cells, and asci are according to Mix essentially the same as described above. The main distinctions between these species are size differences of the asci, stalk cells and conidia.

OBSERVATIONS

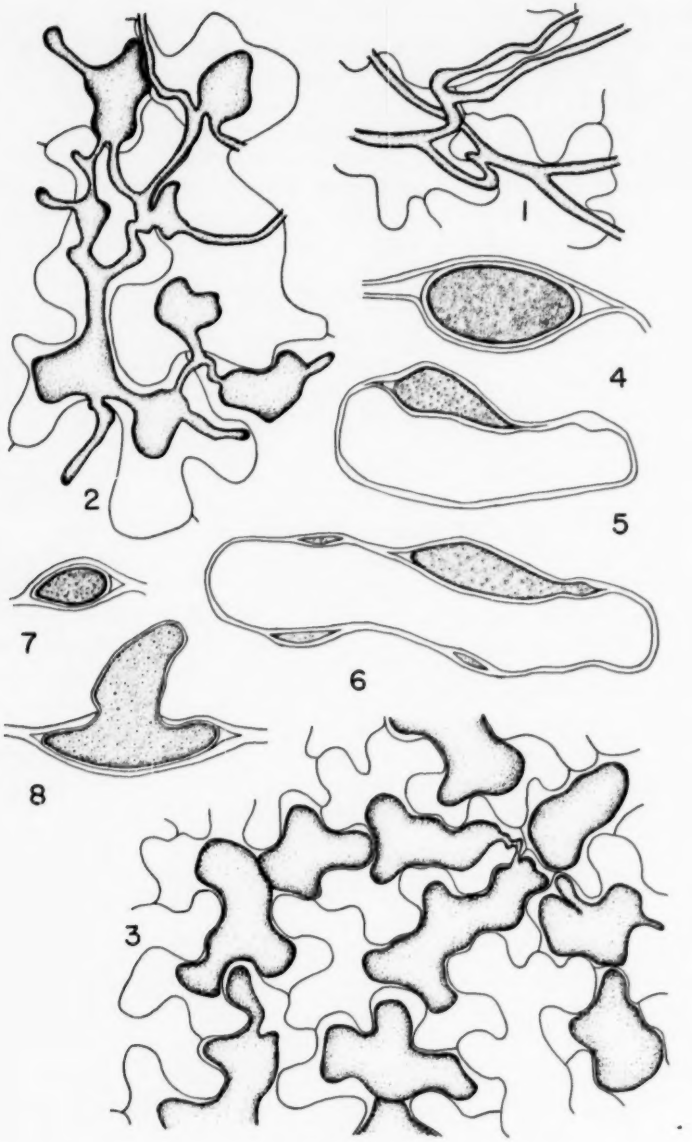
Vegetative mycelium. The vegetative mycelium of *Taphrina higginsii* and *T. osmundae* [2] is composed of fine-branching hyphae located within the cell walls of the host tissue. This mycelium occurs either in the internal leaf tissues, where it progresses throughout the mesophyll within the cell walls, or in the epidermal cell walls, where it forms rather large locules (FIGS. 4–7). Hyphae occurring in the mesophyll are usually very wide but thin, somewhat "bandlike" as described by Butler (**1911**).

The mycelium contains many extremely small nuclei and is only occasionally septate. It is rather narrow at first (FIG. 1), but later forms irregular swellings at irregular intervals (FIG. 2). The enlarging swellings become separated into chlamydospores comparable to those of *Protomyces* and *Taphridium* (FIG. 3). Remnants of the connecting hyphae may remain attached to the mature chlamydospores. Mix (**1947** and **1949**) referred to these chlamydospores as ascogenous cells, comparable to those of *Taphrina*, to which he assigned this species.

The chlamydospores are irregular in shape and often conform to the outline of the epidermal cells (FIG. 3). As they enlarge, the inner portion of the epidermal wall, which forms one wall of the locule, is forced inward into the cell cavity, sometimes nearly obliterating it (FIGS. 5–6).

Formation of the fruiting structure. The spore sac is formed by a small papilla which arises from the chlamydospore and breaks through the upper portion of the host wall (FIGS. 8–10). The papilla is formed by the extension of the thin wall of the chlamydospore. The wall of the chlamydospore never ruptures, allowing an inner membrane to emerge to form the spore sac, as occurs in the germination of the chlamydospores of *Protomyces* and *Taphridium*. As the papilla enlarges, the cytoplasm containing the many small nuclei migrates into

[2] The names *Taphrina higginsii* and *T. osmundae* will be used for convenience of reference. The taxonomic interpretation of these organisms will be found in the conclusions.



FIGS. 1–8.

it and is oriented into a layer next to the outer wall (FIGS. 11–12). A central vacuole is usually present from the beginning and enlarges as the spore sac matures.

During the elongation of the papilla, a cross wall is formed near its base which cuts off a short stalk cell that is empty at maturity. The cytoplasm of the young spore sac is at this stage very homogeneous but becomes more granular as the central vacuole enlarges.

By the time the young spore sac reaches the stage of spore formation, the central vacuole is very large and the cytoplasm is located in a thin peripheral layer (FIG. 12). This fertile layer of cytoplasm is then separated from the vacuole by the formation of a wall which produces a sterile, columella-like structure (FIG. 13). There is usually a small amount of cytoplasm that remains inside after the wall is formed (FIGS. 13, 14, 17). Spores are produced in the fertile layer, although cytological details involving their formation could not be obtained because of the extremely small size of the nuclei. The mature spores are released by the disintegration of the peridium, leaving them exposed in a single layer covering the inner wall (FIGS. 15–16). The spores are 2–5 × 1.5–4 μ and ovate to obovate in outline. They often adhere to each other at their base, forming a large single layer of spores.

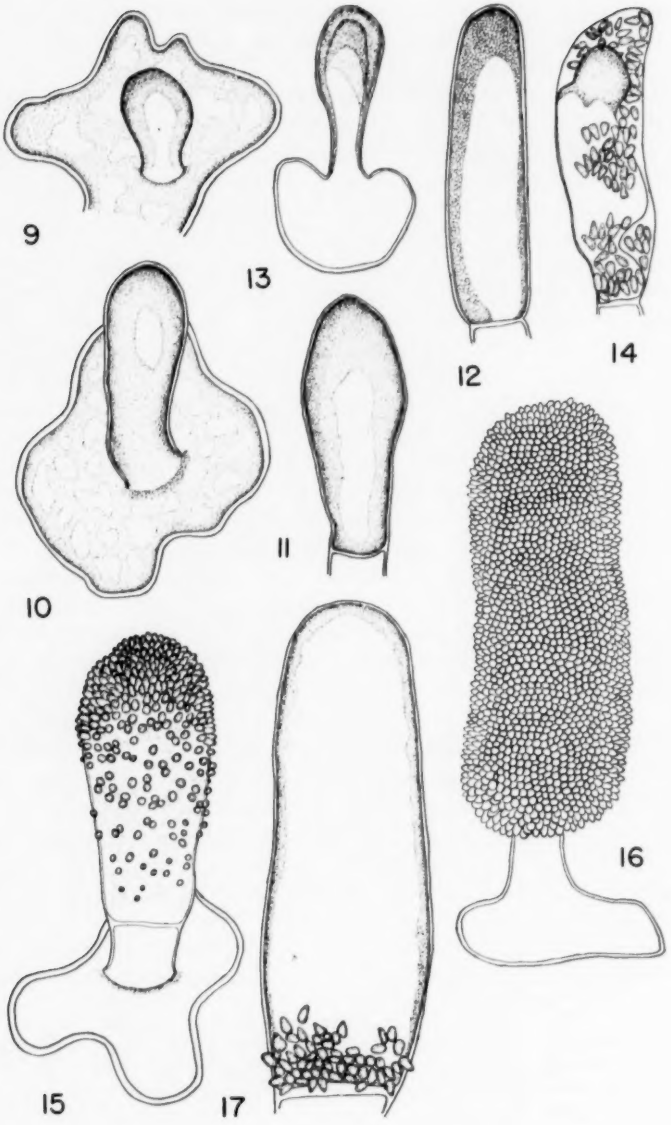
The foot of the ascus that Mix (**1947**) described is apparently only the wall of the chlamydospore that has contracted and pulled away from the inner surface of the locule. Haustoria, described by Mix for this species, have not been found in the material examined.

DISCUSSION

Taphrina osmundae and *T. higginsii* exhibit some features characteristic of Phycomycetes and others of Ascomycetes. This poses a question regarding their placement in a scheme of classification. The characters that would suggest a phycomycete relationship are the multinucleate and rarely-septate mycelium and the formation of a wall within the fruiting structure (spore sac) similar to the columella of the Mucorales.

Those features which would indicate a relationship to the Ascomycetes are most similar to those of the Protomycetaceae, a family which

FIGS. 1–8. *Mixia osmundae*. 1. Vegetative mycelium as it appears on a portion of stripped host epidermis, × 930. 2. Mycelium forming irregular swellings in locules of the host epidermal cell walls, × 425. 3. Swellings separated into individual thin-walled chlamydospores, × 425. 4–7. Various stages in the formation of mycelium and chlamydospores in the host cell walls; numerous small nuclei present in the mycelium and chlamydospores, × 930. 8. Emergence of papilla from a chlamydospore with nuclei and cytoplasm migrating into papilla, × 1395.



FIGS. 9–17.

includes the two genera *Protomyces* and *Taphridium*. However, the Protomycetaceae have been treated in a number of different ways by various authors, not all of whom consider them Ascomycetes.

Bessey (**1950**) followed Fitzpatrick (**1930**) by placing the Protomycetaceae among the Phycomycetes, but was unsure of their natural relationships. Gäumann (**1926** and **1949**) following von Büren (**1915**) considered the fruiting structure of the Protomycetaceae as a synascus and placed these fungi in the order Taphrinales of the lower Ascomycetes. According to Gäumann and von Büren, each nucleus within the synascus became oriented around the periphery and formed what he called a spore mother cell. This nucleus divided, possibly by meiosis, and formed the four ascospores of a single naked ascus. He contended that the synascus contained numerous naked asci composed of a tetrad of ascospores and was thus distinct from a normal sporangium of the Phycomycetes. Bessey (**1950**) believed that these could not be called asci since nuclear fusion did not occur before the formation of the spores. He makes this statement on the assumption that nuclear fusion occurred at the time of conjugation of the spores. Although conjugation does occur with regularity in some species, karyogamy has not yet been definitely demonstrated in either *Protomyces, Taphridium, Taphrina higginsii* or *T. osmundae*. The mycelium of *Protomyces* was described by von Büren (**1915** and **1922**) as intercellular and composed of multinucleate septate hyphae. Although the mycelium of *Taphrina osmundae* and *T. higginsii* is multinucleate and occasionally septate, it has a completely different habit. It develops within the cell walls of the internal tissues, the lateral walls of the epidermal cells, or the outer walls of the epidermal cells. This type of mycelial habit also occurs in several species of *Taphrina*.

In *Protomyces* and *Taphridium*, chlamydospores are formed by the intercellular mycelium. In both genera they are formed within the tissues of the host plant. However, in *Protomyces* the chlamydospores are scattered irregularly throughout the host tissues, whereas in *Taphrid-*

FIGS. 9–17. *Mixia osmundae*. 9–10. Papilla emerging from chlamydospore with large central vacuole, × 930. 11–12. Young spore sac with large central vacuole and stalk cell, × 930. 13. Young spore sac with cytoplasm in a layer next to wall with formation of columella-like inner wall separating most of the cytoplasm from the central vacuole, × 930. 14. Mature spore sac showing inner columella-like wall and outer peridial wall still present, × 930. 15. Mature spore sac with outer peridial wall absent, × 930. 16. Mature spore sac with columella-like wall typically covered with spores, × 425. 17. Columella-like wall of mature spore sac with most of spores disseminated; small amount of cytoplasm remaining within columella-like wall, × 930.

ium they are formed in a continuous sub-epidermal layer. The ascogenous cells of all species of *Taphrina*, as well as the chlamydospores of *T. osmundae* and *T. higginsii*, are formed at the surface of the host.

The chlamydospores of *Protomyces* and *Taphridium* are three-layered with a thick exospore and a thin mesospore and endospore. Germination is accomplished by the rupture of the outer walls, allowing the inner membrane to emerge and form the spore sac. However, in *Taphrina osmundae* and *T. higginsii* the spore sac is formed by a papilla which arises as an extension from the thin wall of the chlamydospore. The ascus in *Taphrina* may either be formed by the rupture of the ascogenous-cell wall, or else this wall may stretch and elongate without rupturing.

As the spore sac in *Protomyces* and *Taphridium* develops, a large vacuole begins to form in the central portion and confines the cytoplasm to a peripheral layer. A very similar condition sometimes exists in *Taphrina*. There is also a large central vacuole formed in the fruiting structure of *T. osmundae* and *T. higginsii* However, before spore formation occurs in the latter, a wall replaces the membrane separating the large central vacuole from the cytoplasm, a process resembling columella formation in the Mucorales.

Spore formation in all of these organisms occurs in the peripheral layer of cytoplasm. In many species of *Taphrina* vacuoles form around uninucleate portions of cytoplasm which delimit spores by the fusion of the inner portion of the vacuolar membranes. A wall is then secreted to form the ascospores. However, in the Protomycetaceae and *T. osmundae* and *T. higginsii*, the method of spore formation is unknown.

Nuclear behavior in the Protomycetaceae is not known. Bessey (**1950**) stated that the spores conjugate through a conjugation tube and the two nuclei fuse to form a diploid nucleus. Although conjugation of spores is reported by DeBary (**1887**), von Büren (**1915** and **1922**), Fitzpatrick (**1930**) and Gäumann (**1949**), nuclear fusion remained a question with them. In the latest work on *Protomyces*, Tubaki (**1957**) reported copulation of spores in *P. pachydermus* but not in *P. iouyei* and *P. lactucae-debilis*. However, he stated that the nuclei, even of the conjugated cells, were so small that details could not be observed.

There appear to be two alternatives concerning the nuclear history in the Protomycetaceae, *Taphrina osmundae* and *T. higginsii*. Nuclear fusion may follow copulation of the spores, resulting in diploid nuclei in the mycelium and spore sac, with reduction to the haploid condition preceding spore formation. The other alternative is that the two nuclei of the two united spores do not fuse but remain in conjugate pairs

throughout the development of the mycelial phase. In this condition, karyogamy probably occurs in the spore sac, with immediate meiosis to produce the haploid condition of the spores. These two possibilities are based on the assumption that conjugation of the spores does occur; however, this may not be necessary in all species, since copulation is not known to occur in some forms. If this is true, then there may be present a nuclear history similar to that found in many species of *Taphrina* (except *T. epiphylla*) where the conjugate pairs of nuclei arise from the single haploid nucleus of an ascospore or blastospore. Copulation would then not be essential to the life history of these organisms.

In *Taphrina* a single conjugate pair of nuclei occurs in the ascogenous cell, which is perhaps comparable to the chlamydospore of *Protomyces*. There is then only one fusion nucleus, which gives rise to the ascospores of an ascus. Gäumann compared the naked asci in the synascus of *Protomyces* to the single ascus of *Taphrina*, and because of this considered them to belong to the same order of Ascomycetes, the Taphrinales.

The mycelium and the young chlamydospores of *Taphrina higginsii* and *T. osmundae* contain a large number of very minute nuclei. However, neither nuclear fusion nor meiosis has been observed. At best it can only be postulated that a type of spore formation similar to that of *Protomyces* occurs here. The mature spores occur in a single layer between the inner columella-like wall and the outer wall. In *Protomyces* also they are formed in a single layer next to the outer wall. However, the inner boundary is the membrane of the central vacuole instead of a definite wall, as in *T. higginsii* and *T. osmundae*.

Most of the species of *Taphrina* produce a stalk cell which is separated from the ascus by a septum. In the species which have been studied cytologically, the stalk cell is considered to represent a vegetative cell of the diploid generation. Although *T. osmundae* and *T. higginsii* form stalk cells, little is known of their true nature and the nuclear behavior involved in their formation. The presence of the stalk cell in these organisms is a distinguishing feature, since it is not present in *Protomyces* and *Taphridium*.

In *Protomyces* and *Taphrina*, the spores are forcibly discharged, whereas they are released by the disintegration of the outer wall in *T. osmundae* and *T. higginsii*.

CONCLUSIONS

As discussed above, *Taphrina osmundae* and *T. higginsii* exhibit many similarities to both the Protomycetaceae and the Taphrinaceae.

However, the multinucleate condition of the mycelium and young fruiting structures and the apparent similarity in spore formation seem to indicate a closer relationship to the Protomycetaceae than to the Taphrinaceae. Because of this and other morphological similarities, these organisms are tentatively included in the family Protomycetaceae.

The presence of the columella-like wall, the septum which cuts off the stalk cell from the spore sac, and the mycelium which occurs in the walls of the host cells require that these organisms be maintained as a separate genus in the Protomycetaceae. Therefore, it is necessary to erect a new genus for these organisms. The name *Mixia*, in honor of Dr. A. J. Mix who has contributed so much to the study of the Taphrinales, especially the genus *Taphrina*, is hereby assigned to these fungi.

MIXIA gen. nov.

Ascocarpium deest; mycelium multinucleatum occurrens in loculis intra muros cellularum hospitis et formans chlamydosporas amplificatas tenuiter tunicatas in loculis cellularum epidermalium hospitis; chlamydosporae germinantes formantes saccum sporarum ab cellula basali septo separatum; paries in sacco sporarum formata separans vacuolum centralem ab cytoplasmate multinucleato; sporae numerosae in zona peripherali cytoplasmatis.

Ascocarp lacking; mycelium multinucleate, occurring in locules within the cell walls of the host, forming enlarged thin-walled chlamydospores in locules of the outer walls of the host epidermal cells; chlamydospores germinating to form a spore sac separated from a stalk cell by a septum; a wall in the spore sac separating the central vacuole from the multinucleate cytoplasm; numerous spores in a peripheral layer of cytoplasm.

TYPE: *Taphrina osmundae* Nishida.

The species *Taphrina higginsii* described by Mix (**1947**) is considered identical with the species previously described by Nishida as *T. osmundae*. The only apparent difference between these two forms is that the former occurs in the United States on *Osmunda cinnamomea* L. and the latter in Japan on *O. regalis* L. var. *japonica* Willd. Mix reported a small difference in the size of the spore sac but this was not found to be consistent nor is it considered a basis for specific distinction.

Mixia osmundae (Nishida) comb. nov.

Basionym: *Taphrina osmundae* Nishida, Miyabe Festschrift 167, 206. 1911.

Synonym: *Taphrina higginsii* Mix, Mycologia **39**: 75. 1947.

Mycelium at first only occasionally septate, multinucleate and occurring in the cell walls of the internal tissues or of the epidermal cells of the host; mycelium in locules of outer walls of the epidermal cells form-

ing large, thin-walled chlamydospores, forcing the inner layers of the cell wall into the cell cavity, sometimes nearly obliterating it; spore sac arising as a papilla by the stretching of the chlamydospore wall and separated from the stalk cell by a septum; numerous ovate to obovate spores arising in a peripheral layer of multinucleate cytoplasm separated from the central vacuole by a wall; spores released by disintegration of the peridial wall; spore sacs 40–80 × 13–23 μ; spores 2–5 × 1.5–4 μ.

Causing small to large, yellowish to light brown, unthickened spots on leaves of *Osmunda regalis* L. var. *japonica* Willd. and *O. cinnamomea* L.

DISTRIBUTION: United States (Georgia, Michigan), and Japan.

COLLECTIONS EXAMINED: United States on *Osmundae cinnamomea* L.: Hamilton, Georgia, Pine Mountain, Blue Springs Farm, May 26, 1938, *B. B. Higgins* (TYPE specimen of *Taphrina higginsii*); same location, June 11, 1955, *C. L. Kramer* (*TK-236*).

Japan on *Osmundae regalis* L. var. *japonica* Willd.: Pref. Iwate, Mt. Iwate, June 13, 1934, *K. Togashi* (Herb. Morioka Imp. Coll. Agric. and For.); Kyusu, Mt. Kirisama, May 29, 1938, *I. Hino* (Herb. Lab. Path. Veg. Miyazaki Koto Norni-Gukko); Japan, July 1912, *K. Yoshino* (Herb. Agric. and Dendrol School, Kamo, Niigata-Ken); Japan (?), May 30, 1900, *K. Yoshino;* Kiyozumi, June 25, 1954, *A. J. Mix;* Kuyozimi, June 1956, *K. Tubaki* (specimen preserved in FPA).

SUMMARY

A new genus in the Taphrinales has been described and assigned the name *Mixia*. Because of the similarity of the mycelium and the fruiting structure, this organism has been tentatively placed in the family Protomycetaceae.

The characters which distinguish this genus from the other two genera of Protomycetaceae, *Protomyces* and *Taphridium*, are: the presence of the "columella-like" wall in the spore sac; the septum which cuts off the stalk cell from the spore sac; and mycelium which occurs in the walls of the host cells.

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STUDIES ON SECOTIACEOUS FUNGI. VIII. A NEW GENUS IN THE SECOTIACEAE RELATED TO GOMPHIDIUS.[1, 2]

ALEXANDER H. SMITH AND ROLF SINGER

(WITH 9 FIGURES)

The fungi here described are interesting because they clearly indicate a connection between the genus *Gomphidius* of the Agaricales and the Secotiaceae of the Gastromycetes. Also, all the species have been found in a single geographic area, the western United States. This area is of considerable general interest because of the large number of other secotioid Gastromycetes known to occur in it.

The species described in the following account could be placed easily in the two main subgenera of Singer's (**1949**) classification of *Gomphidius* were it not for the fact that the spores are not discharged from the basidia in the manner typical of Hymenomycetes, and the hymenophore does not become oriented for spore discharge. In addition, the hymenophore has many chambers, lined by hymenium containing fertile basidia, which do not open to the outside, so that spores could not possibly escape from them. In other words, the morphology of the fructification is that of the Secotiaceae. Because of these gastromycete features, we are describing the two new species in the Gastromycetes but recognizing that their relationships are with *Gomphidius*.

The name *Brauniellula* was selected to indicate the resemblance of this genus to *Brauniella* in certain microscopic characters. This does not necessarily imply that we believe the two genera are intimately related. As we pursue the evolutionary lines of development evident in the Agaricales into the Gastromycetes (or vice versa depending on one's views in the matter) we hope to shed more light on this problem.

The field work during 1958 was financed by the University of Michigan Herbarium. Previous work in the area, which laid the ground work for the 1958 expedition, was financed jointly by the Faculty Research Fund of the University of Michigan and the Na-

[1] Papers from the University of Michigan Herbarium and the Department of Botany No. 1088.

[2] Published out of order of receipt as excess pagination through subsidy by funds from the National Science Foundation.

tional Science Foundation. With the continued destruction of our virgin forests in the United States and the removal of this set of characteristic habitats from our land, it is highly desirable to inventory their entire flora at the earliest possible date because of the possible extinction of many species. The agencies which sponsor this type of work are thus filling an urgent need at a critical time.

Brauniellula gen. nov.

Gastrocarpio obtuse companulato vel convexo aut centro depresso, peridio glabro vel fibrilloso; gleba sublamellari vel lacunosa, loculis frequenter elongatis irregularibusque, columellae adnata variabiliterque decurrente vel libera (columellam haud attingente); columella percurrente; velo praesente vel absente; sporis eis *Gomphidiorum* analogis; cystidiis eis *Gomphidiorum* simillimis vel ab eis paulum distinctis magnitudine, forma, reactionibus. SPECIES TYPICA *B. nancyae.*

Gastrocarp obtuse to campanulate or convex, at times depressed, surface glabrous to fibrillose; gleba sublamellate to lacunose, the cavities often elongate and irregular in shape, attached to columella and attachment extending various distances down it, at times an opening produced by slight expansion of the peridium freeing the lower margin of the peridium from its attachment to the stipe-columella or free from columella; columella percurrent; veil present or absent.

Spores large and resembling those of species of *Gomphidius,* cystidia resembling those of *Gomphidius* in size, shape, and color reactions or deviating only slightly from this pattern.

KEY TO SECTIONS AND SPECIES

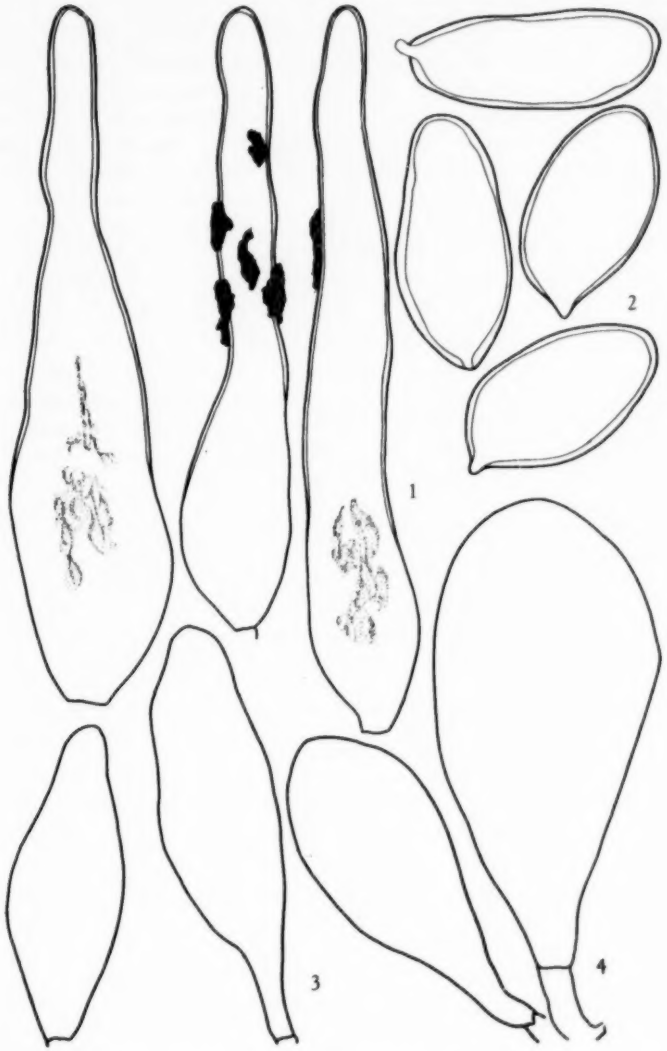
1. Flesh white at first; stipe with lemon-yellow base; spores remaining dark smoky brown in KOH.....Sec. *Gomphidius* (*B. leucosarx* only species known)
1. Flesh ochraceous to mineral red at first; stipe ochraceous to vinaceous throughout; spores becoming pale brownish to melleous in KOH.....Sec. *Brauniellula*
   2. Cystidia as revived in KOH with a vinaceous-red content.....*B. nancyae*
   2. Cystidia with hyaline content as revived in KOH.....*B. albipes*

Section **Gomphidius** sec. nov.

Sporis non-pseudoamyloideis, stipite deorsum citrino, peridio tenui, intus albo. SPECIES TYPICA: *B. leucosarx.*

Brauniellula leucosarx sp. nov. FIGS. 3, 4, 6 and 8

Gastrocarpio 15 mm lato, pallide vinaceo, mox atro-maculato; peridio tenui, intus albo, in aere exposito vinaceo-alutaceo; gleba griseola, loculata, libera; stipite cum columella 12 × 6 mm., intus alba, solida, laesa tarde pallide purpurascente, basi intus extusque citrino; sporis 15–19.8 × 7–9 μ, atrofumosis KOH iodique ope;



FIGS. 1–4, spores and cystidia. FIG. 1, pleurocystidia of *B. nancyae*; FIG. 2, spores of *B. nancyae*; FIGS. 3–4, pleurocystidia of *B. leucosarx*.

cystidiis 65–90 × 18–35 μ, clavatis vel fusoideo-ventricosis, statu vivo saepe purpurascente-incrustatis; hyphis haud gelatinascentibus, defibulatis.

Gastrocarp 15 mm broad, convex-depressed, surface with debris adhering to it but apparently not viscid, shape irregular, margin lobed, ground color pale vinaceous but surface soon blackish spotted; peridium thin, interior white but slowly becoming tinged vinaceous buff when cut, odor and taste not distinctive; gleba drab-gray, oval in longitudinal section, consisting of minute chambers, no gill-structure visible, *free from columella to apex of gastrocarp*, peridium curved in around the gleba at the lower edge so that the latter is not truly exposed to the outside but no veil is present; stipe-columella 12 × 6 mm, solid, white within but slowly becoming pale vinaceous, base lemon yellow inside and out, slowly dark grayish-violet in Melzer's sol. (but individual hyphae not amyloid under microscope).

Spores 15–19.8 × 7–9 μ, smooth, smoky brown in both KOH and Melzer's sol., walls slightly thickened, with no apical discontinuity but occasional spores with bifid apex, oval to elliptic in face view, obscurely inequilateral in profile view, apex rounded; basidia mostly 4-spored, a few 2-spored, 50–60 × 10–14 μ, clavate, when fresh the content nearly lemon yellow in Melzer's sol., dull yellow as revived in Melzer's, hyaline in KOH; cystidia 65–90 × 18–35 μ, clavate to fusoid-ventricose, apex rounded to obtuse, wall thin or with slight irregular thickenings, when fresh often incrusted with amorphous material which is vinaceous red in KOH, dingy yellowish as revived in KOH; tramal plates of hyphae 5–9 μ in diam. and with short cells, floccose, interwoven, subhymenium absent—the basidia originating in the tissue of the tramal plate; peridium of loosely arranged floccose hyphae 4–9 μ in diam., the cells not much inflated but many heavily incrusted with yellowish to brown material (in KOH), no gelatinous hyphae seen anywhere; clamp connections none.

Solitary under *Pinus contorta*, Louie Lake Trail, Payette National Forest, Idaho, July 31, 1958, Sm-59316, TYPE; *Nancy Jane Smith* collector.

Near the lower edge of the gleba sections of the latter show a slight lamellar structure, but the main glebal body is truly lacunose. Although known from only a single fructification, the latter was in perfect condition and there is no reason to doubt the data taken from it. These positive data are exceedingly important since it is the first gastroid type connecting up the *Gomphidii* of the subgenus *Gomphidius* with secotioid types. The fruiting body was found in an area where *Rhizopogon rubescens* and *Brauniellula nancyae* also occurred, both typical members of the lodgepole-pine flora of central Idaho. Hence we consider it very

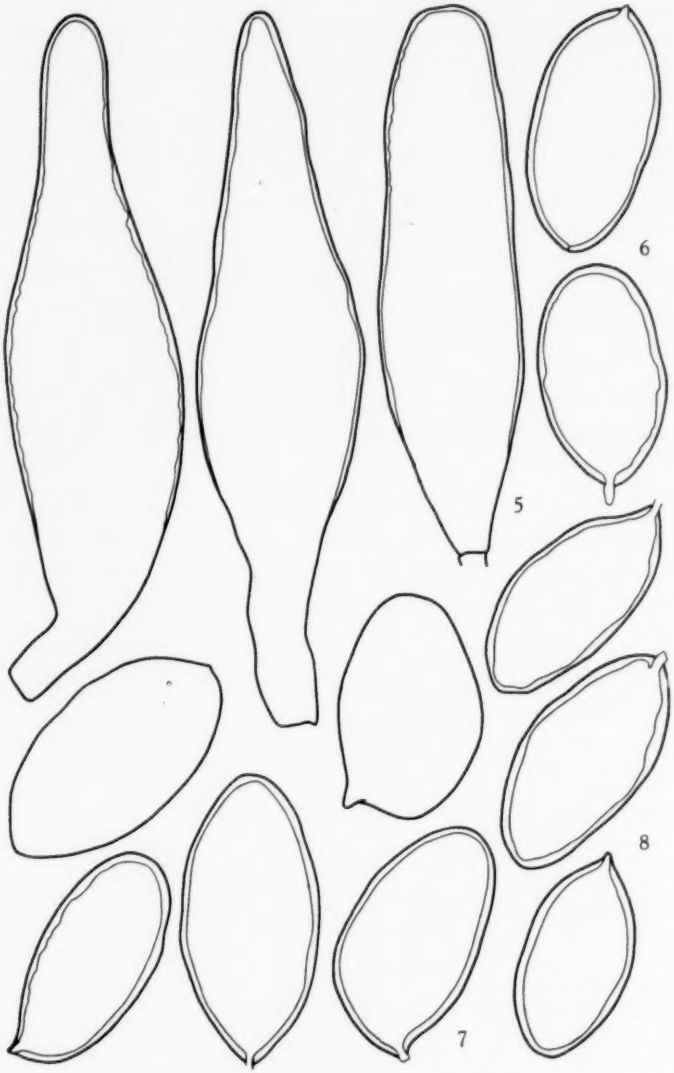
probable that *B. leucosarx* forms mycorrhiza with lodgepole pine. It is interesting to note that the cystidia are less cylindric than in the related species of *Gomphidius,* but that the color of the spores is typical of that group. The characters which relate this species to Gomphidii of the subgenus *Gomphidius* are: the yellow base of the stipe which turns dark in Melzer's, but, as in *G. glutinosus,* no amyloid reaction is visible under a microscope, the typical gomphidioid spores, the vinaceous incrustation of the cystidia in KOH on fresh material, and the white flesh of the peridium and stipe-columella above the yellow base. If one chooses to disregard the gastromycete nature of the fruiting body, it still does not fit any species of *Gomphidius.* It would seem to be, in some respects, a connection to *G. septentrionalis,* in which a glutinous veil is only slightly developed, but the cystidia and lack of a veil amply distinguish it. A similar relationship to *G. maculatus* is suggested by the white flesh and lack of a veil, but in that species the cap is viscid, the spores are larger and its cystidia give different color reactions.

Section **Brauniellula**

Brauniellula nancyae Smith sp. nov. FIGS. 1, 2 and 9

Gastrocarpio (5–)10–50 mm lato, margine demum a stipite-columella separato sed constanter decurvato; peridio appresse fibrilloso, sublubrico ut in *Inocybe geophylla* sed pellicula gelatinosa destituto, fibrillis griseolis supra fundamentum ochraceum, aetate vinaceo-purpurascente, crasso et ex eo agriciformi (ut pileus *Gomphidii* cuiusdam); gleba convoluto-loculato vel sublamellari ochracea, dein grisea, plerumque velo fibrilloso ochraceo vel vinaceo margineque peridii obtecta; stipite-columella 3–15 × (5–)8–10 mm aequali vel ad basin attenuata, ochracea, demum vinoso-rubra, et velo fibrilloso-striato; sporis 16–20 × 6.5–9 μ, ellipsoideis vel oblongis, levibus, in aqua fumoso-flavo-brunneis, in KOH pallide melleis; cystidiis 100–150 × 14–26 μ, subventricosis vel subcylindraceis, apice attenuatis obtusis vel subacutis, in statu vivo purpureo-incrustatis; fibulis nullis.

Gastrocarp (5–)10–50 mm broad, obtusely campanulate to convex or depressed, margin irregular and often lobed and at first connected to stipe-columella by a thin fibrillose veil of ochraceous to vinaceous fibrils —i.e., a true veil—margin of peridium becoming free from the stipe-columella in age but remaining decurved, surface dry and appressed fibrillose or when wet merely subviscid to the touch as in *Inocybe geophylla*—no gelatinous pellicle present—fibrils grayish to dark drab, ground color ochraceous and in age slowly changing from ochraceous to vinaceous to purplish red; peridium thick and resembling the context of an agaric cap, ochraceous to ochraceous-orange in young fresh fruiting bodies, bluish black in Melzer's sol. fresh, in $Fe(SO_4)$ very quickly turning black, in KOH becoming red or darker purplish red, odor and



FIGS. 5–8, spores and cystidia. FIG. 5, pleurocystidia of *B. albipes;* FIGS. 6 and 8, spores of *B. leucosarx;* FIG. 7, spores of *B. albipes.*

taste not distinctive; gleba a convoluted mass of loculate to lamellate-intervenose tissue, the portion of the gleba becoming exposed usually appearing somewhat lamellate, very few of the interior cavities actually opening to the outside and hence spore discharge non-functional if it actually does occur, typically remaining completely covered by the veil and the incurved margin of the peridium but in a few gastrocarps opening out slightly to expose the lower portion of the gleba, color ochraceous at first but in age drab from the spores; stipe-columella 3–15 mm long, (5–)8–10 mm thick at apex, equal or narrowed below, solid, ochraceous over all but in age finally vinaceous red, streaked with ochraceous to vinaceous fibrils from the dry veil, base often reddish from these fibrils.

Spores 16–20 × 6.5–9 μ, in face view elliptic to narrowly elliptic, in profile showing a slight suprahilar flattening, smooth, wall thickened slightly (less than 1 μ thick), smoky yellow-brown in H_2O mounts of fresh material, *pale mellcous* in KOH either in fresh or revived material, strongly pseudo-amyloid (dark red-brown) in Melzer's sol. in either fresh or revived material, no apical differentiation observed; basidia 4-spored, 44–52 × 9–12 μ, dull orange-brown to yellowish in Melzer's sol., hyaline and with "granular" content fresh; cystidia abundant, 100–150 × 14–26 μ, subventricose to subcylindric, more or less tapered to an obtuse or subacute apex, walls flexuous toward apex, thin-walled, when fresh with vinaceous-red incrustations around medial area in age, when revived in KOH, content vinaceous red, yellowish-hyaline in Melzer's sol.; hyphae of tramal plates 4–8 μ in diam., subparallel and curving out slightly to an interwoven subhymenium, the hyphae thin-walled, with scattered incrusting particles some of which are reddish as revived in KOH, *some hyphae distinctly though weakly amyloid* (with blue to lilac walls) in fresh material treated with Melzer's sol., reaction very erratic in dried material and appearing absent on some specimens; hyphae of the "cuticle" 4–5 μ in diam., radially arranged, much incrusting material present and this reddish in KOH on revived sections; hyphae of context hyaline but in sections revived in KOH the section showing a pinkish tint, mostly not incrusted; clamp connections none.

Solitary to cespitose under *Pinus contorta*, throughout central Idaho, TYPE collected at Pen Basin, Payette National Forest, Idaho, Aug. 5, 1958, *Nancy Jane Smith*, Sm-59644.

Additional Material: The following collections were made during the summer of 1958 from Heaven's Gate Ridge, Nez Perce National Forest roughly on a line extending southeast to Stanley, Idaho, at the northeast edge of the Sawtooth Mountains. Sm-58838; 58977; 58978; 58979; 58992; 59194; 59310; 59326; 59335; 59448; 59480; 59644; 59794; 59867; 59944; 60083; 60219; 60441; 60477; 60511.

Our first experience with this fungus was a single collection by Smith from Iron Creek, near Stanley, Idaho, in late August 1954, from under lodgepole pine. The gastrocarps were so contorted, however, that the detailed structure was not clearly evident. During the season of 1958 an expedition to the same area was made and a detailed search made for additional collections. The 1958 season was apparently very favorable for the development of this species, for, thanks largely to the efforts of Miss Nancy Jane Smith, we found it at Stanley as well as in nearly every stand of lodgepole pine visited after the 10th of July until late August. The collecting data indicate conclusively that the species is associated with *Pinus contorta,* very likely as a mycorrhizal associate. Its pattern of occurrence is interesting. Very frequently it occurs in or next to clusters of carpophores of *Rhizopogon rubescens,* which is also very abundant in the association, and like the *Rhizopogon,* development is hypogeous until near maturity when the fructifications at times become partly exposed. In most fructifications the development is angiocarpic, the gleba never becoming exposed, but during the height of the fruiting period some specimens were observed in which the veil had broken and the gleba had become partly exposed by a slight expansion of the "cap." No spore deposits were obtained from such specimens though several attempts were made.

The gleba varies from truly lamellate to truly lacunose and all intermediate stages are readily found in large fruitings. However, the most erratic character is the amyloid reaction of the hyphae of the peridium and tramal plates. In fresh material a weak but distinct blue reaction is observed on some hyphae. These are numerous enough to be easily seen and cause the dark appearance resulting from the application of Melzer's sol. to the cut surface of the flesh. This can be readily reversed by the application of bases or even weakly alkaline tap-water, so that it often appears to be easy to "wash out" the reaction with several changes of water. When sections of material which has been dried are revived directly in Melzer's sol., one gets, especially if the mount is crushed by pressure on the cover glass, a reaction *in places* in both context and tramal plates, to bluish or bright or dull lilac. If the sections are not crushed a few hyphae may turn blue or there may be no reaction whatever. About the only really distinctive feature of this behavior is that with the technique used the color change took place, but one could not be sure which hyphae would react. Actually it closely resembles, both in its pattern of behavior and the color produced, that found in *Gomphidius* among some of the species of the subgenus *Chroogomphus* Singer, as described by Smith and Dreisinger (**1954**).

FIG. 9. Fruiting bodies of *B. nancyae*, about natural size.

This gastromycete is perhaps most closely related to *Gomphidius leptocystis* and *G. helveticus* by virtue of its dry, fibrillose pileus, the red reaction in KOH of the incrustations of the hyphae and the content of the revived cystidia, the shape of the cystidia and the fact that these structures have thin walls, and the gradual change to purplish red as the fructification ages. All of its characters, including the spores, are

so obviously those of the subgenus *Chroogomphus* that the affinity with it cannot be questioned. A significant feature of the spores, however, is that the color in 3 per cent KOH mounting medium fades out appreciably. Hence, one studying only herbarium specimens revived in KOH might be inclined to question whether the color of the spores ever was typical of *Gomphidius*. The strong pseudoamyloid reaction is a constant character for mature spores but immature ones remain yellow to pale yellow-brown.

Brauniellula albipes (Zeller) comb. nov. FIGS. 5 and 7

Secotium albipes Zeller, Mycologia **40**: 675. 1948.

Gastrocarp up to 50 mm in diam., subglobose, surface viscid, smooth, glabrous; red, drying dark mineral red, not breaking away from the stipe below; peridium very thin, context brown, rather hard (?); gleba loculate, chambers small, somewhat dehiscent from base of columella leaving at maturity a small ring-hole, broad in cross section, pale ochre-stramineous; stipe-columella turbinate, tapering to a thin acute base from a broad apex, 10–15 mm long, solid, percurrent; no volva seen.

Spores 14.5–20 × 7.5–10 μ, ovate to elliptic in face view, obscurely inequilateral in profile view, with a short eccentric basal apiculus and a slight suprahilar depression, wall slightly thickened and pale brown in KOH, content hyaline and slightly reticulate, no apical differentiation observed, smooth to faintly wrinkled (not completely revived ?), pale ochraceous tawny to near tawny in Melzer's sol. (hence faintly to distinctly pseudoamyloid when mature, at times (oldest spores?) with a darker episporium and a subhyaline endosporium visible, not metachromatic in cresyl blue.

Basidia 34–48 × 10.5–12 μ, cylindric-clavate, with 2, 3, or rarely 4 sterigmata, the latter unequal in size, some small, some large, some almost straight, others curved and thicker below; cystidia scattered, 80–140 × 15–25 μ, subcylindric to fusoid-ventricose with an obtuse to rounded apex, walls thin to slightly thickened (up to 1.5 μ), smooth or with some granular incrustation, not reddish in KOH; hymenophoral trama and trama of the peridium consisting of filamentous to rather broad hyphae mixed with occasional oleiferous elements, frequently regular in the tramal plates but sometimes with lateral stratum of arcuate-diverging hyphae, and in some places somewhat gelatinized although not showing a well differentiated external gelatinized layer or a gelatinized lateral stratum but filaments often wavy; hyphae of the external layer of the peridium partly (not all) incrusted by an epicellular amyloid (blackish violet) or amylaceous mass which tends to disappear gradually after repeated hydrolization (reduction); some hyphae near

the cap surface with granular amyloid contents; hyphae with clamp connections, but these not readily demonstrated in all mounts.

In rich forest duff, Merrimac, Butte County, California, Nov. 9, 1932, leg. *Thelma Norman*, det. E. E. Morse as *Secotium erythrocephalum* (NY, ex Zeller Herb., two portions of TYPE).

We have used Zeller's original description for the macroscopic details but have added our own observations on the type material. Morten Lange has annotated the type, and his observations agree with ours. In the first place, the gleba is not dark brown and the spores are not truly ornamented, and the gelatinization is less extensive than the diagnoses would make one think. The similarity with *Weraroa erythrocephala* is only in the color of the peridium, and even so the color is quite a different red. Whether the surface material on the stipe, which makes it appear white, is an artifact, we cannot decide but think it is entirely possible. Unfortunately neither of us nor Zeller has or had seen this material or any other of this species in the fresh condition, and it is possible that the stipe is colored when fresh. There seems to be a fibrillose "partial veil."

In spite of the fact that the species epithet may be a misnomer, the fungus is most interesting in the light of the two species previously described. We place it beside *B. nancyae* in the subgenus *Brauniellula* because of the following characters: 1) Spore characters, such as the large size, thickened wall with no other apical differentiation, the pale color in KOH and the pseudoamyloid reaction; 2) the large cystidia similar in size and shape to many of those found in subg. *Chroogomphus* of *Gomphidius;* 3) the vinaceous-red color of the peridium; and 4) the amyloid reactions of the tramal and peridial hyphae. Microscopically it is at once distinguished from *B. nancyae* by not having the content of the cystidia red as revived in KOH. As compared in the dried state the characters of the stipe also separate them but here no real comparison can be made because of lack of data on *B. albipes*.

In *B. albipes* the spores are less pseudoamyloid than in *B. nancyae* or in species of *Gomphidius* of the subgenus *Chroogomphus*, the cystidia lack the chemical reaction in KOH of *B. nancyae* and hence are less "gomphidioid," and the characters of the stipe in dried material are not comparable to those of *B. nancyae* or of *Gomphidius*. These features taken together indicate that *B. albipes* is farther removed, in the evolutionary scale, from *Gomphidius* than is *B. nancyae*. In fact, *B. albipes* might also be compared with *Brauniella* (Singer **1953**, **1955**). At this time, however, especially in view of the data presented in this series of

papers, we believe the relationships of the Secotiaceae need not be rediscussed before the situation has been studied on a monographic level.

DEPARTMENT OF BOTANY
UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN; AND
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LITERATURE CITED

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NOTES AND BRIEF ARTICLES

A new species of Dacrymyces from Honduras

Among the many collections made by Professor C. J. Alexopoulos in Honduras during the summer of 1958 were two of a striking species of *Dacrymyces* which appears to be previously undescribed.

Dacrymyces dictyosporus sp. nov.

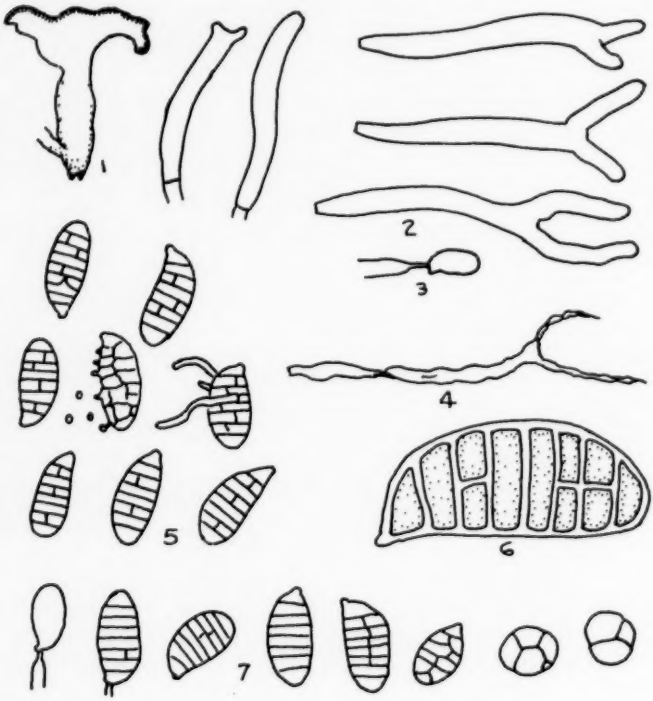
Aurantiacus, gregarius, suberumpens, pulvinatus, 5–13 mm diam. confluens ad 35 mm longus, siccus ochraceus vel sordide rufus, intus semipellucidus, mollissime gelatinosus e hyphis hyalinis tenuibus; hymenio rugoso-plicato vel cerebriformi; probasidiis clavatis, 45–70 × 7–10 μ, basidiis furcatis; basidiosporis late et obtuse fusiformibus, transverse 7-septatis et 4–8-septatis longitudinaliter, (22.5–)25–28 (–30) × (9–)10–12(–13.5) μ.

Bright orange, drying dull orange to dull red, tough-gelatinous, becoming horny but not contracting greatly when dry and remaining conspicuous; basidiocarp at first pezizoid, deeply rooted in bark, becoming irregularly lobate, anastomosing early and forming a conspicuous elongate fruiting up to 35 mm in length and 7 mm in width, the surface cerebriform; cortex with a few swollen hairs at margin of hymenium but mostly little differentiated; internal hyphae with slender lumens, septate, without marked bulbous enlargements or clamp-connections; probasidia clavate, 45–70 × 7–10 μ; basidia furcate; basidiospores broadly and bluntly fusiform, early transversely 7-septate, with 4–8 or more longitudinal septa (2–4 usually visible on one side), the longitudinal septa frequently beginning to appear while the spore is still on the basidium, (22.5–)25–28(–30) × (9–)10–12(–13.5) μ, germinating by the production of minute conidia, about 2 μ in diameter, or by germ-tubes, or rarely subglobose, about 15 μ in diameter, to broadly oval, 17–20 × 12–14 μ.

Honduras: Mt. Uruyu, Zamorado, alt. 4500 ft., 17 July, 1958, *C. J. Alexopoulos 344*, TYPE; same locality, 20 July 1958, *C. J. Alexopoulos 345*. On bark of *Pinus oocarpa*. In herb. IA.

No. 345 is the younger of the two collections, showing less anastomosis and a somewhat larger proportion of the subglobose and oval spores. These are very few, however, as compared with the very numerous subfusiform spores.

There are four species of *Dacrymyces* described as having muriform spores. *D. ovisporus* Brefeld, Unters. **7**: 158. 1888, has broadly elliptical spores not exceeding 15 × 11 μ, very much like the occasional subglobose spores found in the Honduras specimens. Brefeld gives the size as 20–25 × 15 μ, but his scales are known to have been inaccurate. *D. longisporus* Brefeld, Unters. **7**: 158. 1888, occurring with *D. ovisporus* on the same substratum, has spores greatly resembling those of



FIGS. 1–7. *Dacrymyces dictyosporus*. FIGS. 1–6, Type. 1. Section through fructification, × 3. 2. Basidia in various stages, × 500. 3. Tip of epibasidium showing young spore on clearly marked sterigma, × 500. 4. Collapsed basidium, × 500. 5. Eight spores, one germinating by production of conidia, one by germ-tubes, × 500. 6. Single spore, showing broad septa, × 1450. 7. Eight spores from No. 345. At left, a young spore and a mature spore still on sterigmata, the latter already showing one longitudinal septum; at right, three subglobose and oval spores.

FIGS. 2–5 and 7 drawn with aid of camera lucida.

D. dictyosporus. They are pictured as having 7–9 transverse septa and about the same proportion of longitudinal septa as in *D. dictyosporus*. Furthermore, Brefeld's dimensions, 35–40 × 15 μ, when suitably reduced, would probably give spores of the approximate size of *D. dictyosporus*. However, *longisporus* is described as fruiting as a cluster of minute yellow pustules, each the size of a pinhead. This cannot apply to *D. dictyosporus*. *D. subalpinus* Kobayasi (Tokyo Bunr. Daig. B **4**: 120. 1939. *f. 4, M*) has more fusiform spores 35–37 × 15–16 μ with 15–16 transverse septa in addition to the longitudinal ones and is described as pulvinate, soft-gelatinous within and occurring on angiosperm wood. On the basis of Kobayasi's description I cannot refer the Honduras collections to his species. *D. rubidus* Holtermann (Myk. Unters. Trop. 55, *pl. 7, f. 13–15*. 1898) is so poorly described that it is difficult to say what its characters are. Saccardo and Sydow in Sacc. Syll. Fung. **16**: 221. 1902, compiled a description from the figures, describing the spores as reniform, becoming 4–6-septate, 25 × 6–7 μ. They say nothing about the subsequent longitudinal and oblique septa. Holtermann's *f. 15* shows seven spores germinating, the majority of which appear to have had seven primary septa. A much larger proportion of the additional septa are shown as oblique than is the case in the Honduras collection and I should make the longest spore about 30 μ in length on the basis of the magnification given. The length of these spores is in substantial agreement with that of those of the Honduras collection but they are definitely narrower and different in shape. In view of the difficulty of deciding what Holtermann had from his description and the minor but possibly significant differences between the Honduras collection and the little that is known about *D. rubidus*, I think it wise to designate the Honduras material as new.

D. dictyosporus has the aspect of a luxuriant development of *D. palmatus*, from which it differs in the much larger, muriform spores and in its simpler cortex. The germinating spores found on the surface of the basidiocarp (FIG. 5, center) appeared to have produced additional septa and were germinating by the production of minute spherical conidia on short stalks. The spores germinating by production of germ tubes (FIG. 5, right) were from sections left in distilled water over night.

Professor Lorene L. Kennedy, of the University of Alberta, kindly examined some of this material and I am indebted to her for a number of helpful suggestions.—G. W. MARTIN, State University of Iowa, Iowa City.

THE FUNCTION OF TAXONOMY IN MYCOLOGY [1]

A taxonomic system is generally considered to have two functions. The first function is to provide an index to species. Taxonomic categories—genera, families, and orders—are pigeon-holes in which species may be filed and by means of which they may be located again for future reference. The second function is to show the phylogenetic relationships among these species. Taxonomy, then, is concerned with the naming, classification, and identification of species and with phylogeny.

What is perhaps a more basic function of a taxonomic system may be implied in the definition of these first two functions, but because of its importance, it should be stated separately and given proper emphasis. This function is to provide a classification, not of species, but of mycological data. Taxonomy is the science of synthesis. Its function is to assemble data from the various sciences of morphology, cytology, physiology, and genetics and to integrate these data in a useful system. Taxonomic categories are much more than mere compartments into which species may be placed. The Erysiphales, the Uredinales, the Peronosporales, for example, are more nearly scientific laws than scientific pigeon holes. Each of these names is a shorthand expression of a great mass of mycological data. The characterization of each order is, although imperfectly so at present, a generalization from a great many facts concerning a great many fungus individuals. If a fungus belongs in the Uredinales, then at once a great deal is known in a general way of its physiology and ecology as well as its morphology. This is true also of lesser categories such as families and genera. The characterizations even of species may well be considered generalizations from the facts concerning groups of individuals.

Taxonomic work, theerfore, is not a preliminary phase of naming species, through which mycology had of necessity to pass and which should now be de-emphasized. It is rather this narrow conception of the function of taxonomy which should be de-emphasized. A useful taxonomic system is the end of mycology, and so long as new data are being produced by morphological and physiological studies, these data must be integrated in this system. Stability in the system of classification is impossible. Criticisms directed against essential revisions, therefore, are without basis. No such limitation is placed on any other science. What physiologist, for example, would accept as valid criticism a complaint that his work was making inadequate the knowledge acquired in the classroom ten, twenty, or thirty years ago? Changes in

[1] Paper No. 349, Journal Series, Georgia Experiment Station.

the system of classification represent hypotheses as to relationships among mycological data; and these hypotheses, like all hypotheses, are important, not only in indicating relationships among existing data, but in pointing out future lines of research.

Taxonomy, moreover, is not a mere academic pursuit. The system of classification is of immense practical importance. Since it represents a summation of mycological knowledge, it is exactly as important as the whole science of mycology. The function of the taxonomic system is to organize this knowledge and to present it in a readily available form for use. Since the system as a whole is of importance, any fact that contributes to this system may be considered to be of immediate practical importance, although it may not be so in itself. Research may be justified on the vague basis that, while the results have no immediate application, some day they may have, and work cannot be restricted to lines that show promise of immediate usefulness. But this is not necessary. It may equally well be said that these results contribute toward the improvement of a system which is of great practical importance and in their relationship to this system they acquire immediate significance.

The objection may be raised that the system of classification is useful in supplying names for fungi under consideration in various phases of mycological work, and in other fields as well, and that constant change in the system is detrimental to this function. The very existence of taxonomic categories, however, is a refutation of the argument that the system is designed primarily for the purpose of giving names to fungi. If the only consideration were to arrive at a name to apply to a particular fungus, any artificial key to species would suffice, and the various higher categories would be largely superfluous. The existence of these categories implies a series of generalizations from the facts of mycology, broadening from species through genus, family, and order to class. Admittedly the naming of fungi is an important function of the taxonomic system and one that should not be overlooked. It should not, however, obscure the greater usefulness of the system in supplying information concerning fungi rather than merely names to apply to them, nor should the desire for a stable nomenclature impede the progressive organization of new data in this system. In a comprehensive treatise on the Pyrenomycetes, Munk [2] arrived at a satisfactory solution to the problem presented by the dual function of the taxonomic system. In his organization of the various taxa he made significant contributions toward the development of a natural system of the Pyrenomycetes. At the same time he attempted to satisfy the practical demands of identification by

[2] Munk, A. 1957. Danish Pyrenomycetes. Dansk. Bot. Ark. 17(1): 1–491.

providing an artificial key to genera that was entirely independent of the taxonomic arrangement he presented.

It may be argued that, since determinations of phylogenetic relationships among species must be based upon the facts of morphology, physiology, and genetics, the same end will be attained regardless of whether the approach is one of establishing a natural, or phylogenetic, system or one of establishing a useful organization of mycological data. Any classification presupposes the existence of a natural system by which the relationships in structure and function among fungi are explained on the basis of common ancestry. The goal of reproducing this system and tracing the multitudinous lines of descent, however, is exceedingly doubtful of attainment; and the difficulty of the task leads to an understandable tendency toward conservatism. Consideration of the great mass of data prerequisite to the establishment of a natural system makes immediate attempts to attain it, even in small groups of fungi, appear premature. The attempt to establish a useful classification of mycological data, on the other hand, has as its goal no static perfection. It recognizes that, from the nature of science, such a goal is unattainable, but that at each step of its development mycological knowledge, imperfect though it may be, is of service. Its goal is a taxonomic system which presents this knowledge in a convenient form as it develops, a system of expanding usefulness.—E. S. LUTTRELL, Georgia Experiment Station, Experiment, Georgia.

OLPIDIUM SYNCHYTRII SP. NOV., A PARASITE OF SYNCHYTRIUM NAMAE

In the course of a study of *Synchytrium namae* Karling its sporangia became infected with a parasite which develops small endobiotic holocarpic zoosporangia, posteriorly uniflagellate zoospores and fairly thick-walled resting spores like species of the chytrid genus *Olpidium*. Accordingly, this parasite is assigned to this genus and described as a new species because of the minute size of the zoospores and its unusual host.

Olpidium synchytrii sp. nov.

Sporangiis hyalinis, laevibus, ovalibus, 8–10 × 11–15 μ, vel sphaericis, 6–20 μ diam., ex uno brevi latere tubulo 3.8–5 × 5–15 exeunte. Zoosporis sphaericis, 1.8–2.2 μ diam.; flagello 7–9 μ longo. Sporis perdurantibus hyalinis; laevibus, sphaericis, 5–16 μ diam., vel ovalibus 5–7 × 8–14 μ; zoosporis germinatione ortis.

Sporangia 1 to 5 per host cell, hyaline, smooth, ovoid, 8–10 × 11–15 μ, or spherical, 6–20 μ, with one exit tube 3.8–5 μ diam. by 5–15 μ long, which usually does not extend much beyond surface of host cell; excep-

tional ones up to 15 μ long and curved; sporangia sometimes discharging zoospores within host cell. Zoospores spherical, small, 1.8–2.2 μ, with a minute hyaline refractive globule; flagellum 7–9 μ long. Resting spores hyaline, smooth, spherical, 5–16 μ, or ovoid, 5–7 × 8–14 μ; forming zoospores directly in germination.

In the sporangia of *Synchytrium namae*, Austin, Texas, U.S.A. TYPE: slide no. 7, Purdue University.

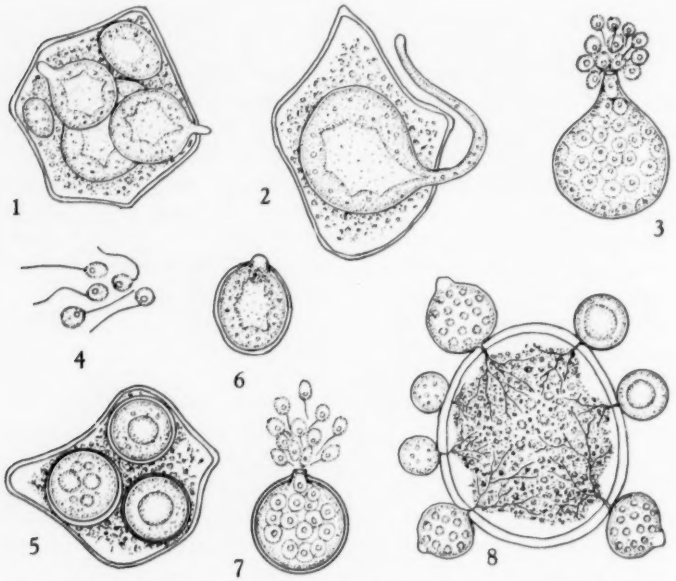
The source of this parasite is unknown, but the circumstances of infection suggest that it may have been present in the soil surrounding the *Nama jamaicensis* plants which were infected with *S. namae*. Such plants were dug up with a ball of soil, planted in pots and transferred to the Purdue greenhouses. *Nama jamaicensis* is largely sessile with its lower leaves in contact with the soil, and these leaves are usually splattered with soil particles during a rainfall or in watering in the greenhouse. Such leaves, which were abundantly infected with *S. namae*, were placed in sterile charcoal water in petri dishes for a study of sporogenesis in the sporangia of *S. namae*, and under these circumstances the sporangia became infected.

As shown in FIGS. 1–7 the life cycle of *O. synchytrii* is basically similar to that of other species of *Olpidium*, and need not be described in detail. As a result of infection the sporangia of the host lose their brilliant orange color, and the protoplasm becomes almost hyaline. As the parasites enlarge the protoplasm decreases in amount and eventually becomes clumped around them (FIGS. 1, 2).

Attempts were made in this study to infect the sporangia of *S. macrosporum* and *S. fulgens* with the zoospores of *O. synchytrii*, but the results were negative, suggesting that it may have a limited host range.

Olpidium synchytrii differs from the other known species of *Olpidium* principally by its minute zoospores, which are only 1.8–2.2 μ in diameter and have a very short (7–9 μ) flagellum. In this respect it resembles most closely *O. algarum* var. *brevirostrum* Sorokin, whose zoospores and sporangia have been calculated to be 1 μ and 4 × 6–9 μ, respectively. Sorokin (**1883**), however, gave no measurements of his fungus, and the sizes noted above were calculated from his drawings. Unfortunately, the sizes of the zoospores are known in only about one-half of the described species of *Olpidium*, so that extensive comparisons cannot be made, but in most of them the zoospores are approximately twice the diameter of those of *O. synchytrii*. The sporangia and resting spores of this species also are quite small, but I do not regard their sizes as very specific and diagnostic. In many other species of *Olpidium* they may be quite small, particularly when several occur in a single host cell.

Olpidium synchytrii also resemble quite closely species of *Rozella* in the size of its zoospores. However, in this genus the sporangium fills the host cell so fully that its wall may be indistinguishable from that of the host (Karling, **1942a**, **b**, **1944**). Single sporangia of *O. synchytrii* also (FIG. 2) have been found in host cells, but in no instances did they fill the host cell completely as in *Rozella*.



FIGS. 1–7. *Olpidium synchytrii*. FIG. 8. *Rhizophydium carpophilum*. FIG. 1. Host sporangium with 5 parasites. × 500. FIG. 2. Large sporangium with curved exit tube. × 500. FIG. 3. Large sporangium discharging zoospores. × 600. FIG. 4. Zoospores. × 500. FIG. 5. Host sporangium with 3 resting spores. × 500. FIGS. 6, 7. Germinating resting spores. × 500. FIG. 8. Resting spore of *Synchytrium linariae* parasitized by *Rhizophydium carpophilum*. × 400.

So far only one other species of *Olpidium*, *O. uredinis* (Lagerheim) Fischer, has been reported as a parasite of a fungus. Lagerheim (**1888**) found it in the uredospores of *Puccinia airae*, *P. violae* and *P. rhamni*, but he was unable to infect the uredospores of other rusts with it. Its sporangia, zoospores and resting spores are considerably larger than those of *O. synchytri*, and the two species do not appear to be identical.

In connection with this description of *O. synchytrii* it may be noted

that I have found that the thick-walled resting spores of *Synchytrium linariae*, *S. fulgens* and *S. macrosporum* may be sparingly or abundantly infected by another chytrid species which I interpret to be *Rhizophydium carpophilum* (Zopf) Fischer. This species occurs fairly commonly on the oogonia and oospores of several water molds, and its occurrence on the resting spores of *Synchytrium* is not surprising. In several cultures of *S. linariae* which had been set up for resting-spore germination, the infection attained epidemic proportions and killed most of the spores. As a result of infection the coarsely granular protoplasm of the host becomes clumped around the branched rhizoidal system, and the residue gradually disintegrates, as shown in FIG. 8. The only other known rhizidiaceous parasite of *Synchytrium* is *Phlyctochytrium synchytrii* which Köhler (**1924**), Harder and Uebelmesser (**1955**), and Scholz (**1958**) found on the resting spores of *Synchytrium endobioticum*, but *R. carpophilum* differs from it by the lack of an endobiotic apophysis.

This study has been supported by a grant from the National Science Foundation.—JOHN S. KARLING, Department of Biological Sciences, Purdue University, Lafayette, Indiana.

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WESTON'S LEPTOMITACEOUS FUNGUS IN FLORIDA

In the course of studies of the aquatic fungi in a series of sinks near Tallahassee, Florida, during the summer of 1957, an interesting fungus belonging to the order Leptomitales was found. As the description of this organism does not appear in the literature, it was assumed that this

was a new genus. Soon after the description of the Florida isolate had been completed, it was learned that Dr. W. H. Weston had previously found it in Louisiana, Central America, and Africa. He will validate this new genus in a future publication. From communications and slides shown at the AIBS meeting in Stanford, apparently this fungus is the same as the Florida isolate.

The present note, then, is for the purpose of calling to the attention of mycologists the occurrence and availability in North Florida of this new genus of the Leptomitales. The fungus is readily obtainable from various fruits and vegetables (apples, bananas, carrots, lemons, oranges, turnips, etc.) placed in traps beneath the surface of the water. Living or preserved material can be supplied on request.

Growth of the highly variable thallus of this new species is apparently unlimited. A more or less definite basal cell is usually present with a highly branched system of rhizoids. Pedicellate zoosporangia appear early in the life cycle, become interspersed with oogonia after a few weeks, and then finally disappear completely. Oogonia alone are present after the first month. Antheridia have not been observed and oosphere germination has not been seen.

The presence of pedicellate reproductive structures, a basal cell, cellulose walls, and oogamous sexual reproduction indicate that the fungus belongs in the Leptomitales. The basal cell and rhizoidal system lead to further classification in the family Rhipidiaceae.—J. J. STUEHLING, JR., AND A. W. ZIEGLER, Florida State University, Tallahassee, Florida.

ERRATA—VOL. 50

In the article on A. J. Mix, p. 325, last paragraph, 4th line from below: For "researches" should be read "researchers."

In the article on "The philosophy of taxonomy," p. 331, 3rd line: "B" and "A" should be transposed.

In the article on "The biosynthesis of chloramphenicol," pp. 491, 493, 495: The running head should read "GALLICCHIO AND GOTTLIEB."

REVIEWS

INTERNATIONAL CODE OF NOMENCLATURE OF BACTERIA AND VIRUSES—BACTERIOLOGICAL CODE, by The Editorial Board of the International Committee on Bacteriological Nomenclature. 186 pp. Iowa State College Press, Ames. 1958. Price, $3.50.

The problems facing the microbiologist attempting to give the correct name to an organism in which he is interested are not necessarily lessened by the appearance of the "1958 Revised Edition" of the International Code of Nomenclature of Bacteria and Viruses. It represents a revision of the International Bacteriological Code of Nomenclature, the English text of which was of much more modest proportions (Journal of Bacteriology **55**: 287–306. 1948; Journal of General Microbiology **3**: 444–462. 1949). This third Code of Nomenclature is coordinate with, and for bacteriologists and virologists presumably replaces, the existing Zoological and Botanical Codes.

The volume is provided with a foreword detailing the history and development of the Code, the International Committee on Bacteriological Nomenclature, and its Judicial Commission; a preface consisting in the main of acknowledgments; and a table of contents. There follow four chapters (General Considerations, Principles, Rules and Recommendations, Provisions for Modification . . .), four appendices (Transliteration of Greek Words into Latin Form . . . , Choice of Spelling between Orthographic Variants . . . , Opinions Relating to Nomenclature . . . , Lists of Connserved and Rejected Names), and a good index. Following most items in each of the first three chapters appear often lengthy but unofficial Annotations citing examples and noting corresponding Rules and Recommendations of the Botanical and Zoological Codes. That these Annotations were either drawn up at different times or by different persons is evident in that the Articles cited for the Botanical Code are sometimes taken from the Stockholm Code (e.g., Principle 12, Rule 8) and sometimes from the Paris Code (Rules 2 and 6); in the instances cited there is no indication of which Code was meant.

Mycologists will presumably be pleased to learn that the Principles, "Rules and Recommendations of this Bacteriological Code for the most part agree with those of the Botanical Code." In large part these are taken verbatim—or with only minor changes—from the Botanical Code Latin diagnoses are not required for new taxa. Such terms as "name,"

"legitimate," "illegitimate," "correct," "effective publication" and "valid publication" are used with the denotations of the Botanical Code, not of the Zoological Code (Principle 5). Suffixes for the formation of names of taxa between subclass and genus are identical with those of the Botanical Code, not the Zoological Code (e.g., *-aceae* for families, not *-idae; -oideae* for subfamilies, not *-inae*) (Rule 4). For taxa which have been transferred or altered in rank, the original author is cited in parentheses followed by the name of the author who effected the alteration (Rule 16).

There are, however, major differences between the Bacteriological and Botanical Codes. Under the Bacteriological Code, the name of a bacterial taxon is to be rejected if it is a homonym of the name of a protozoan taxon (it may be homonymous with the name of any other animal taxon) (Principle 3). The subgenus is the only subdivision to be recognized between genus and species (Rule 5 Annot.). Further, genus and subgenus are coordinate nomenclaturally, i.e., subject to the same rules and recommendations (Rule 5b), and of "equal priority status" in each rank (Rule 22b Annot.). The subgenus is further considered to be uninomial rather than an epithet, and it may not be a homonym of another genus or of another subgenus in another genus (Rule 5 Annot.).

Mycologists may be startled to learn that "The words subspecies and variety are alternative designations for the same taxonomic rank; they are synonyms" (Rule 7 Note [2]). In conformity with the treatment of subgenera and genera, subspecies (varieties) and species are considered coordinate nomenclaturally and of "equal priority status" in each rank (Rule 22c Annot.). (There seems to be a conflict between this treatment and Principle 9, which states that "In species the correct name is the binary and in subspecies the ternary combination of the generic name with the earliest available legitimate epithet validly published with the same [*sic*] rank.") Trinomial nomenclature is permitted: "One may write *Bacillus subtilis* subsp. *niger* or *Bacillus subtilis* var. *niger* or *Bacillus subtilis niger*" (Rule 7 Annot.).

The rules do not determine the naming of taxa below the rank of subspecies (variety), which are termed "infrasubspecific subdivisions," but a series of terms designate these taxa: strain, biotype, serotype, morphotype, phagotype, group, phase, forma (or *forma specialis*), variant, mutant, stage, state (Rule 8). A recommendation (Rec. 8a) on the use of these terms is provided, which introduces (in Annotations) an additional term, "subgroup," and definitely equates two of the proposed terms (state = stage).

Because of the reliance placed upon cultures, it is understandable that "The nomenclatural type . . . of a species or subspecies is preferably an authentic culture, but it may be a specimen or preparation, illustration or description" (Rule 9a).

In contrast with Article 38 of the Botanical Code (Paris), the Bacteriological Code states that "The name of a genus or of a subgenus is not validly published unless it is accompanied (a) by a description of the genus or subgenus, or . . . (e) by a description of one or more species or by citation of a previously and effectively published description of one or more species included in the genus" (Rule 13).

"There is no provision in the Bacteriological Code for the abbreviation of the names of authors of scientific names. In general such abbreviations are unnecessary and inadvisable" (Rule 16 Annot.). Reducing multiple authors to the first plus *et al.* is, however, specifically encouraged (Rule 15a Annot.).

Lists of names to be abandoned as *nomina ambigua, nomina dubia* and *nomina confusa* are to be listed together as *nomina rejicienda* (Rule 24e, f, g), but apparently such a list will not include names to be abandoned because they were based upon abnormalities (Rule 24h). The concept of conserving specific epithets, vigorously argued and defeated at botanical congresses, has been accepted and put into practice by the bacteriologists.

It is indeed in the area of conservation and rejection of names that one may note a fundamental difference between the Botanical and the Bacteriological Codes. Under the Bacteriological Code this appears to be an area of fuzzy thinking with which not even the Editorial Board could cope successfully. It seems clear that the original intention is expressed in Provision 2, unaltered from the wording of the 1948–1949 version of the Code: "To avoid disadvantageous changes in the nomenclature of the genera by the strict application of the Rules of Nomenclature, the Rules provide for a list of names which must be retained as exceptions (nomina conservanda)." When, however, the Functions of the Judicial Commission are stated in Provision 5 (5), greatly expanded over the 1948–49 Provision 4 (2), we note that in the ensuing ten years not only genera are to be considered for conservation and rejection, but also species, families, orders, etc.

This reviewer would like to call special attention to the statement in this list of functions of the Judicial Commission that it was "to establish lists of . . . *nomina conservanda* . . . together with a list of the generic names [specific epithets] against which each name [epithet] is conserved." It is by no means clear whether the lists of conserved and

rejected names provided in Appendix D were in fact prepared by the Judicial Commission or by the Editorial Board. In either case, these lists (with the exception of the single conserved and single rejected family) do not indicate the rejected names or epithets against which the names or epithets are conserved. And the reason is manifest when one consults the Opinions of the Judicial Commission which have formed the basis for these lists. The Commission has seen fit in several instances to conserve names—not *against* other names known to compete, but—against all synonyms having priority (Opinion 8), or *for* certain *taxonomic* concepts (Opinion 7; Opinion 11, *cfr.* Int. Bull. Bact. Nomen. Tax. **1**: 147–166. 1951; Opinion 13). (The corresponding Commission under the Zoological Code also conserves against unknown names which may compete and has occasionally conserved for taxonomic concepts—as in the case of the malaria parasites.)

The concept of rejected names is also significantly different under the Bacteriological Code from that under the Botanical Code. *Nomina rejicienda* are names "which are not to be used, i.e., are to be permanently rejected" (Provision 3). The only names so rejected which may be reinstated are *nomina dubia* upon action by the Judicial Commission. The *nomen rejiciendum* of the Botanical Code, to be rejected *only* when it and the conserved name are considered taxonomically synonymous, apparently has no counterpart in bacteriology. The lists of rejected names of genera and subgenera (Appendix D) include many names which are invalid or illegitimate, and which would therefore not require listing as *nomina rejicienda* under the Botanical Code.

Clearly a Judicial Commission, charged not only with interpretation of the Rules and with issuing Opinions relative to these, but also given (and exercising) the power of enforcing taxonomic conclusions, is a concept wholly foreign to the Botanical Code. It is, however, something our zoological colleagues have learned to live with.

From a publishing standpoint the volume is admirable, being beautifully bound, well printed on high quality paper (though the reasons motivating certain partially blank pages are unclear), and reasonably free of typographical errors.

While it is not the purpose of this review to argue the merits (if any) of the Bacteriological Code, one cannot help but question whether this Code was really necessary, and whether, indeed, it truly serves the interests of microbiologists. This reviewer was not formerly aware that the bacteriologists (including virologists) considered themselves and their problems to be quite so unusual; but we are faced with a *fait accompli:* there are now apparently "three official codes of nomenclature,

one for each of the [*sic*] three segments of biology: botany, zoology and bacteriology (including virology)" (General Considerations 1 Annot.). To the microbiologist whose interests overlap the segments, the additional Code cannot help but be a burden. Are the "special provisions needed for" bacteria of such compelling magnitude that these could not have been handled under the Botanical Code? The very fact that the Bacteriological Code so closely parallels the Botanical Code seems to argue against the necessity for the separate Code: the special provisions for hybrids and for fossil plants seem to have found adequate expression under the Botanical Code. Even the truly significant difference, the formation of a Judicial Commission with nomenclatural (and taxonomic!) powers, might have found incorporation within the framework of the Botanical Code. As the situation now stands, the microbiologist must in each case decide (when working with a bacterium or virus but not when working with a fungus) whether he is at heart a bacteriologist or a botanist, i.e., which Code he will choose to follow.

"Adherence to the provisions of the Bacteriological Code is left to the individual judgment of the microbiologist. Nonconformity seems to be due more to lack of knowledge of the Code or to lack of understanding of its intent than to fundamental disagreement with the provisions themselves" (General Considerations 1 Annot.). To this point the reviewer would comment: well, perhaps. If the new Code does contribute to stability of bacteriological nomenclature, it seems unlikely that the distinctions between its rules and those of the Botanical Code will have contributed. Rather, stability under the new Code will be the result of rule by decrees (Judicial Commission "Opinions") instead of rules of law (the Code).—RICHARD P. KORF, Department of Plant Pathology, Cornell University.

TOPICS IN MICROBIAL CHEMISTRY: ANTIMYCIN, COENZYME A, KINETIN AND KININS, by F. M. Strong. x + 166 pp., 35 figs. John Wiley & Sons, Inc., New York. 1958. Price, $5.00.

This little book contains the full text of a series of three lectures delivered by Professor Strong in 1956 at the Institute of Microbiology, Rutgers University, under the sponsorship of the E. R. Squibb Institute for Medical Research.

The three subjects have little in common except that the substances covered are or may be obtained from microorganisms and in some instances affect or are functional in microorganisms. Thus, antimycin is

an antifungal agent derived from a soil organism of the genus *Streptomyces*. Coenzyme A is an ubiquitous natural form of bound pantothenic acid, is found in a variety of microorganisms as well as in other forms of life, and participates in the energy metabolism of living beings of all types.

The subject matter is presented in clear and concise manner; the viewpoint is strictly that of an isolation biochemist. Little attention is given the microbiological aspects of any of the substances concerned, either with respect to cultural conditions for their production or to their functions in living organisms. The history and steps in isolation of more and more nearly pure materials, with chemical, physical and biological data proving identity of the isolated products, are precisely covered.

For the microbiologist interested in obtaining some chemical background for discussing these three substances and derivatives of them, this book might be very useful. If one is interested in learning how these substances are produced by microorganisms or how they function in them, it would be of no help. The price, moreover, is high for a work with so little scope unless its subject matter is directly concerned with one's research interests.—J. M. MCGUIRE.

MANUALE DI MICOLOGIA MEDICA, by R. Ciferri. Tomo I, 370 pp., 304 figs. Casa Editrice Renzo Cortina, Pavia. 1958. Price, Lira 4000. (About $6.50.)

In Volume 1 of his Manuale di Micologia Medica, Ciferri has laid a broad base for the volume to follow. He has covered, sometimes briefly, sometimes in considerable detail, the history, importance, concepts and technics of medical mycology and the latter's relationship to general mycology. He has outlined the rules of taxonomy which govern the systematic arrangement of fungi and defined the technical terms which must be understood and the criteria which must be observed in identifying fungi. No one familiar with the many contributions Ciferri has made to mycology will be surprised by the careful attention he gives to the hierarchy of taxonomic groups from division down to genus.

The fungi, particularly those which cause human or animal disease, are listed under family headings and many are illustrated. Keys to families and tables indicating relationships or significant characteristics of families emphasize the author's interest in taxonomy. The sapro-

phytic occurrence of the fungus pathogens of man and some details of their ecology are given.

There are sections on the technics of examining specimens and cultures, on staining, preparation of culture media, use of the microscope, purification of cultures, and examination of fungi in pure culture. Serologic aids to diagnosis, production of experimental mycoses in animals, therapeutic agents and biochemistry, genetics and physiology of the fungi, are discussed in varying degrees of detail. Clinical mycology is not covered in this volume.

The book is well bound, on good quality paper, and has numerous useful keys and tables. Illustrations vary considerably in quality. Most of those used will be familiar to readers because of their prior publication in journals or books, but the sources and authorships of these illustrations are credited in only a few instances.—C. W. EMMONS.

TITLES OF SERIALS—All mycologists who are obliged to write or interpret literature citations (are there any others?) will wish to acquaint themselves with an article on "Abbreviations of titles of serials cited by botanists," by Lazella Schwarten and Harold William Rickett, in Bull. Torrey Bot. Club **85**: 277–300. 1958. The introductory pages give clear and cogent reasons for the system of abbreviation that has been the standard, although unfortunately not the universal guide, since 1893; the list of titles and abbreviations is quite surely the best available. The "first principle" presented is one especially deserving of wider adoption: to retain the order of words that actually appears on the cover or title-page: e.g., Brit. Mycol. Soc. Trans., Bull. Soc. Mycol. Fr. Whoever has hunted for a serial in a card index or the Union List of Serials under each of the words in a long title will appreciate the usefulness of this simple convention.

The list is especially called to the attention of contributors to MYCOLOGIA. This is not to say that it is adopted as official. The advantages of having an official list are questionable; and some of the forms adopted —e.g., Rev. Mycol. Paris and Rev. Mycol. Toulouse, rather than the generally accepted Rev. de Mycol. and Rev. Mycol.—are less comprehensible than the alternatives; others—Bull. Torrey Club, for one—seem needlessly pruned; why not then Ann. Missouri Gard.? Nevertheless, it will be found that the great majority of entries are in the best possible form. Those who do not have the journal, or who wish separate copies for greater accessibility, may secure them from Dr. Rickett at the New York Botanical Garden for thirty-five cents.—D. P. R.

BIBLIOGRAPHIE DER PFLANZENSCHUTZLITERATUR 1948–1949, by J. Bärner. xli + 689 pp. Verlag Paul Parey, Berlin, and Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem. 1958. Price, DM 65; also available on exchange.

Twenty-five earlier volumes of this Bibliography of Plant Protection, for 1914–47 and 1950–51, were prepared by H. Mortstatt (through 1939) and Bärner; the present work fills the lacuna. The 21,000 entries are arranged according to subheadings under causes, hosts, and methods, and there is an author index. It is to be hoped that additional volumes will appear, to bring the index up to date.

LITERATURQUELLEN UND IHRE KÜRZUNGEN AUS DER BIBLIOGRAPHIE DER PFLANZENSCHUTZLITERATUR, by J. Bärner. 16 pp., processed. Biologische Bundestanstalt für Land- und Forstwirtschaft, Berlin-Dahlem. 1958.

A very extensive list of serials that have published articles on plant protection since 1913, and preferred abbreviations for the titles. A special characteristic of the list is the frequent employment of the place of publication as a part of the abbreviated citation. The list can be of assistance to workers seeking to run down obscure titles.—D. P. R.

MICRO REPRODUCTIONS—*A Monograph of the Erysiphaceae,* by E. S. Salmon, Mem. Torrey Bot. Club **9**: 1–292. 1900, long out of print and much sought, is available in microcard or microfiche (transparent film 3 × 5 in., similar to microcard) copy from Micro Methods Limited, East Ardsley, Wakefield, Yorkshire, at £1.10.0d (approximately $4.20), plus cost of packing and postage. Other mycological works similarly available are Micheli's *Nova Plantarum Genera,* 1729 (£2.2.0d, $5.90), Fries's *Hymenomycetes Europaei,* 1874 (£3.3.0d, $8.85), and Berkeley & Broome's *Notices of British Fungi,* 1837–1885 (£1.15.0d, $4.90).

MORPHOLOGY OF PLANTS, by Harold C. Bold. xxiii + 699 pages, 561 figs. Harper & Bros., New York, 1957. Price, $8.00.

This is a new kind of textbook, explicitly designed to meet the problem which has arisen as a result of the wide adoption of survey courses in biology. Such courses, broad in coverage but necessarily shallow or sketchy in specific fields, constitute inadequate preparation for advanced work in special areas. It is the author's intention to bridge the gap in

such a way that students who have taken such a survey course may have an adequate knowledge of the wide field of plant morphology, substantially greater than they now get in an introductory course in botany, without excessive repetition of what they may have been expected to retain from the survey course.

Allowing for introductory matter and comments on securing and preparing material for study, about one-fifth of the volume is devoted to fungi. Most mycologists would probably regard this as generous representation.

The author divides the plant kingdom into 24 divisions, giving his reasons for doing so in the final chapter, with further particular comment in connection with his discussion of each division. Even in view of the current tendency to break up the older comprehensive major groupings, this will seem excessive to many. However, as the author is careful to point out, any suggestions as to phylogeny must be regarded as tentative. Certainly a serious and informed attempt to improve our current admittedly inadequate system is welcome.

The bacteria and fungi are grouped in the divisions Schizomycota, Myxomycota, Phycomycota, Ascomycota and Basidiomycota, with the imperfect fungi and lichens treated as artificial groups maintained for the sake of convenience. A good argument can be made for ranking the bacteria as a division, although even in such case reservations are in order. The arguments for making a division for the Myxomycetes are much less convincing and the same is true for the Phycomycetes. The phylogeny of both is complicated by the strong suggestion of protozoan affinity. It would seem that the very strong evidence of close relationship between Ascomycetes and Basidiomycetes is rather summarily dismissed. And to rank Heterobasidiomycetes and Holobasidiomycetes as full classes ignores the now well-known intermediates between these groups.

The book is well written and extensively and, for the most part, admirably illustrated. The figure of *Pyronema* (p. 191) is scarcely convincing; the basidium of *Coprinus* (p. 213) was obviously drawn from a paraffin preparation and no such distorted basidium could possibly discharge its spores; the figure of "*Geastrum*" (p. 218) is clearly *Astraeus*. None of these details is serious.

Whether texts of this type will prove to be effective in remedying the problems developed by the survey courses remains, of course to be decided. The one under consideration deserves wide reading and will be particularly useful to advanced students who have not had a proper introduction to the wide field of plant morphology before entering upon specialized work.—G. W. MARTIN.

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